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The role of nitrogen fixation in intensive forestry in Canada Part II

Research carried out at Laval University, Quebec, on nitrogen-fixing actinorhizal trees and shrubs

J.A. Fortin, L. Chatarpaul, and A. Carlisle

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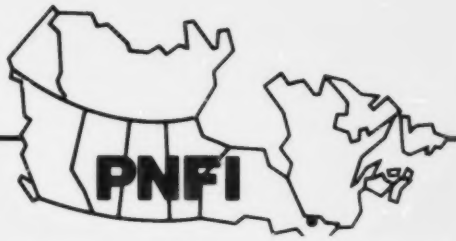

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Cover:
Testing the efficiency of Frankia isolates to infect, nodulate, and fix nitrogen in Alnus species growing in a N-free medium. Note the poor growth of uninoculated plants in the foreground.

THE ROLE OF NITROGEN FIXATION IN INTENSIVE FORESTRY IN CANADA

Part II

Research carried out at Laval University, Quebec, on nitrogen-fixing actinorhizal trees and shrubs

Information Report PI-X-29

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Contents

1	Summary
1	1.0 Introduction
2	2.0 Establishment of plots of alder and other tree species to examine effects on yield and soil fertility (C. Camiré, G. Pregent, and J.A. Fortin)
2	2.1 Objectives
2	2.2 Establishment
2	2.2.1 Sites
2	2.2.2 Tree propagation
4	2.2.3 Experiment design
6	2.3 Site calibration
6	2.4 Survival
6	2.4.1 Pests and diseases (M. Dessureault)
10	2.4.2 Diseases of alders (Alnus) (G. Tardif)
10	2.4.3 Tree nutrition on the peat bog (G. Beaulieu and G. Pregent)
10	2.5 Prediction equations (G. Pregent)
12	2.6 Establishment of plots at Laval University Nursery (C. Camiré and R. Camirand)
12	3.0 The nutrient content of alder litter soils in stands of Alnus rugosa (C. Camiré, I. Girard, and C. Godbout)
13	4.0 Competition between hybrid poplar and black alder (Alnus glutinosa) (C. Camiré, B. Côté, and P. Bellefleur)
15	5.0 Cycling of nitrogen in alder in the greenhouse (C. Camiré and B. Côté)
16	6.0 Growth and survival of different provenances of Alnus glutinosa (L.) Gaertn. (C. Camiré)
19	7.0 Growth of Alnus crispa and Salix on spoil heaps in region LG-2, James Bay, Quebec (C. Camiré)
19	8.0 Allelopathic relationships of alders and poplar (J.R. Thibault, R. Jobidon, and P. Younger)
21	8.1 Phenolic acids in balsam poplar leachates and their role as allelochems

22 9.0 Isolation of superior Frankia strains and their culture, storage, and inoculation (P. Normand and M. Lalonde)

23 9.1 Collection and isolation
23 9.2 Inoculation and culture
25 9.3 Infectivity
25 9.4 Effectivity
26 9.5 Chromatographic analysis of sugars to identify Frankia strains (P. Normand, J.A. Fortin, and M. Lalonde)
26 9.6 Frankia production and mass inoculation (J.A. Fortin, M. Lalonde)
27 9.7 Survival of selected Frankia symbionts in the field (M. Lalonde and D.M. Burgess)

28 9.7.1 Tree and shrub species
28 9.7.2 Frankia inoculation
28 9.7.3 Performance
31 9.7.4 The 1982 experiment

31 10.0 Relationships between actinorhizal symbioses, mycorrhizae, and the rhizosphere (C. Godbout, M. Couture, B. Côté, J.A. Fortin)

32 10.1 Ectomycorrhizae of alder (C. Godbout and J.A. Fortin)
36 10.2 The transfer of nitrogen by alder ectomycorrhizae (M. Couture)
38 10.3 Nitrogen fixation in the rhizosphere (C. Camiré and B. Côté)

39 11.0 Conclusions

39 11.1 Establishment of plots of alder and other tree species
41 11.2 Nutrient content of litter and soils on Alnus rugosa sites
41 11.3 Growth of Alnus and Populus in different mixtures and different spacings
41 11.4 Alder nitrogen budget
41 11.5 Growth and survival of Alnus glutinosa provenances
41 11.6 The growth of alder and willow on borrow pits at James Bay, Quebec
42 11.7 Allelopathic relationships
42 11.8 Isolation, culture, storage, infectivity and effectivity, and mass production and application of superior strains of Frankia
43 11.9 Survival of Frankia symbionts in the field
43 11.10 Relationships between actinorhizal symbioses, mycorrhizae, and the rhizosphere
44 11.11 General conclusions

45 Literature

50 Appendix I
57 Appendix II
67 Appendix III
104 Appendix IV

Tables

5 1. Location and characteristics of the experimental plantations[1]
5 2. Species, propagation, and provenances
7 3. Average physical characteristics of soils in the experiments[1]
7 4. Mean chemical characteristics of the soils[7]
8 5a. Mortality one year after planting, Fall 1981
9 5b. Number of living trees and % mortality in brackets (for 30 trees maximum per plot), Fall 1982
11 6. Diseases of alder (after Tardif 1982)
14 7. Description of ENFOR funded activities in the Laval University nursery
14 8. Concentration of nutrients in leaves of Abies balsamea with or without alder (after Girard and Godbout 1980)
14 9. Nutrient content (mg) of 100 current year's leaves of Abies balsamea with or without Alnus rugosa
17 10. Production of biomass in the greenhouse experiment (individual plant)
17 11. Nitrogen uptake in the greenhouse experiment (individual plant) in mg
17 12. Excess nitrogen NO_3^- from lysimeters in the greenhouse experiment
18 13. Alnus glutinosa provenances used in the experiment
22 14. Phenolic acids in leachates of balsam poplar Populus balsamifera (after Perradin 1981)
24 15. List of provenances from which Frankia strains were isolated
29 16. The Alnus and Elaeagnus species used in the experiment
29 17. Provenances of Alnus and Elaeagnus
29 18. Provenance of Frankia strains
30 19. Alder seedling inventory - Petawawa National Forestry Institute, summer 1981
34 20. List of the fungal isolates used, isolation year, associated host, and degree of ectomycorrhiza formation of 46 species of fungi tested with Alnus crispa, A. rugosa, and Populus tremuloides
37 21. Weight, nitrogen concentration, and nitrogen fixation of mycorrhizal and non-mycorrhizal alder (A. crispa)
38 22. Weight, nitrogen concentration, and nitrogen fixation of mycorrhizal and non-mycorrhizal pine (Pinus strobus)

FOREWORD

ENFOR is the acronym for the Canadian Government's ENergy from the FORest (ENergie de la FORêt) program of research and development aimed at securing the knowledge and technical competence to facilitate, in the medium to long-term, a greatly increased contribution from forest biomass to our nation's primary energy production. This program is part of a much larger federal government initiative to promote the development and use of renewable energy as a means of reducing dependence on petroleum and other non-renewable energy sources.

The Canadian Forestry Service (CFS) administers the ENFOR Biomass Production program component which deals with such forest-oriented subjects as inventory, harvesting technology, silviculture and environmental impacts. (The other component, Biomass Conversion, deals with the technology of converting biomass to energy or fuels, and is administered by the Renewable Energy Branch of the Department of Energy, Mines and Resources). Most Biomass Production projects, although developed by CFS scientists in the light of ENFOR program objectives, are carried out under contract by forestry consultants and research specialists. Contractors are selected in accordance with science procurement tendering procedures of the Department of Supply and Services. For further information on the ENFOR Biomass Production program, contact

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or a CFS research laboratory.

This report is based on ENFOR project P-198 which was carried out under contract (DSS File No. KL011-1-0020) by the Canadian Forestry Service and Laval University.

SUMMARY

A program of work at Laval University was funded by the Canadian Forestry Service's ENFOR program between 1979 and 1983 to provide the scientific and technological basis for future use of nitrogen-fixing plants to maintain soil fertility and increase yield in intensive forestry systems.

Field experiments consisting of Alnus and other tree species on a variety of sites and at different spacings were established for future use. Preliminary results indicated that alders greatly increased the yield of hybrid poplar. Alder also contributed about 40 kg ha^{-1} $year^{-1}$ of litter to the soil and improved the leaf size and nitrogen status of associated Abies balsamea. Nitrification occurred in the acid alder humus (pH 3.9).

Methods were developed to: isolate and culture Frankia symbionts, test their effectiveness, store the symbionts in a gene bank, and inoculate them on a large operational scale (one million alders). The operational method is ready to use. Sporulating and non-sporulating strains of Frankia were differentiated and the ability to sporulate, as well as the spectrum of sugars, has been suggested as a basis for Frankia taxonomy.

Operational use of inoculated alders indicates that a good supply of phosphorus is vital to the success of the alder. Populus balsamifera leaf and bud leachates were found to contain phenolic acids of the cinnamic and benzoic series and had allelopathic effects on alder by inhibiting growth and nodulation, reducing seed germination, and deforming root hairs.

Contrary to the belief that alder is highly specific concerning its ectomycorrhizal symbionts, it was found that both Alnus crispa and Alnus rugosa formed ectomycorrhiza with epidermal Hartig nets in conjunction with several fungal partners. The form of these ectomycorrhizae differed from those on the Pinaceae with cortical nets. Some of the ectomycorrhizal fungi on alder form symbioses with other trees and shrubs. The possibility that the network of hyphae in forest soils act as a pathway for fixed nitrogen was tested by a preliminary experiment using $^{15}N_2$, but the results were inconclusive.

1.0 INTRODUCTION

Part II of this report is concerned with the research program supported by ENFOR funds at Laval University. The program was designed to develop an information base and genetic material upon which biological techniques of soil amendment involving use of nitrogen fixation could be developed.

The work consisted of six projects. The first project was concerned with the establishment of field experiments of Alnus (alder) and other species to permit future studies of the effects of alders on tree fibre yield and soil fertility. This work also examined some of the problems of propagation, planting, and pests and diseases encountered during establishment.

2.0 ESTABLISHMENT OF PLOTS OF ALDER AND OTHER TREE SPECIES TO EXAMINE EFFECTS ON YIELD AND SOIL FERTILITY

(C. Camiré, G. Pregent, and J.A. Fortin)

2.1 Objectives

The aim of the work was to establish plots of alder and other tree species on a variety of sites to examine effects of the alders on yield and soil fertility. Other attempts to mix alders with different species (for example, in southeastern Ontario) encountered difficulties, resulting in uneven survival and growth. It was hoped that the work at Laval University would shed some light upon these problems. While the expectation was that establishment would be sufficiently rapid and successful to permit sites to be used for research during the contract period, the ultimate goal was to provide well-designed experiments, thereby filling the major gap identified in the review of literature in Part I of the report. The review makes it clear that, although many experiments have been carried out to examine effects of rhizobial legumes and actinorhizal non-legumes on tree growth and soil attributes, few were designed for the purpose, and most had drawbacks that impeded their interpretation. These ENFOR plantations would, if successful, be of present and future value.

2.2 Establishment

The plant propagation and plantation establishment was carried out during 1979-80 and 1980-81, with subsequent survival assessment, plant replacement, plant and soil analysis, and plot management in 1981-82 and 1982-83.

2.2.1 Sites

Blocks were located at St-Lambert, St-Louis, Villeroy, and Amos, all in the Province of Quebec. The first three were in the St. Lawrence River valley near Quebec City, and Amos was in the boreal region to the west, north of Val d'Or. All four were situated between latitudes 46°00'N and 48°30'N, and longitudes 69°30'W to 78°00'W (Figure 1).

There were two sites at St-Lambert, one with a poorly drained heavy loam, and the other a peat bog; one site at St-Louis with a loamy soil on what had previously been a farm; and one site at Villeroy where the soil was a well-drained sandy loam. The Amos site had also been a farm and the relatively poor soils varied from a well-drained sandy soil to a poorly drained clay-loam. Before planting all the sites were ploughed and harrowed after removing natural tree regeneration, in order to reduce competition (Table 1).

2.2.2 Tree propagation

The *Alnus crispa*, *A. rugosa*, *Populus tremuloides*, and *Pinus banksiana* were all raised from seed in paper plots (50842) containing peat and sand (2:1). *Alnus glutinosa* seedlings were taken from the 'wild' at the Villeroy Arboretum. The *Salix* spp., *Populus* hybrids, and *Populus balsamifera* were raised from cuttings.

During propagation of *Alnus rugosa* from seed for experimental plots at St-Louis, Villeroy, etc. delays in plant production were caused by the presence of many non-viable seeds. The problem was examined by Fortin and

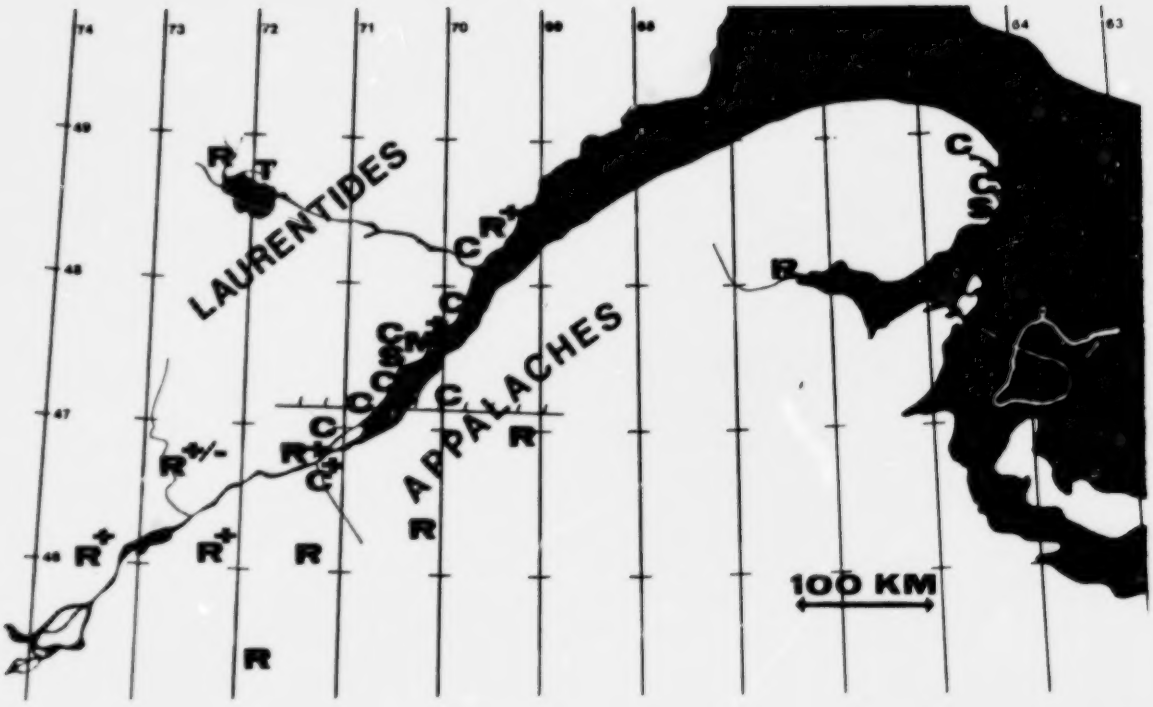

Figure 1. Map of the St. Lawrence River Valley of Quebec, showing the general area studied in the project. "R" and "C" refer to stands of Alnus rugosa and Alnus crispa respectively from which Frankia were isolated. Sporulating and non-sporulating type are designated "+" and "-" respectively.

Dessurault (1982) who observed hypertrophy on flower bracts, and the asci of Taphrina robinsoniana, a fungal pathogen, on flower ovules. Closer examination revealed intercellular hyphae linking the asci, and the presence of collenchymatous tissue and aborted proembryos. There appeared to be a gradient of pathogenicity, some ovules being damaged more than others. It appears that this fungus affects the production of alder seed. However, seeds from northern sites (James Bay area) were much less affected and were used when available.

2.2.3 Experiment design

The details of the design are given in Fortin (1981 a, b). In brief, the establishment of a total of 18 plots each with an area of 0.4 acres (0.16 ha) had been planned but, due to shortages of planting stock, only 14 were completed; five at Amos, three in St-Louis, four at St-Lambert, and two at Villeroy. Each plot was divided into 32 sub-plots, and in each sub-plot there were 90 trees with 1.2 m between rows and 0.6 m between trees in the rows. Nitrogen-fixing alders were placed in alternate rows with the companion trees. There was a space of 2.4 m between sub-plots.

The 19 treatments consisted of seven tree species (Table 2) in 17 combinations, and two controls (weeded and unweeded). The species, provenance, method of propagation are given in Table 2.

The treatments consisted of:

1. Alnus crispa (Ait.) Pursh.
2. A. rugosa (Du Roi) Spreng.
3. Populus tremuloides Michx.
4. A. crispa + P. tremuloides
5. A. rugosa + P. tremuloides
6. Populus hybrids (USA M52, M53 clones)
7. A. crispa + Populus hybrids
8. A. rugosa + Populus hybrids
9. Salix spp.
10. A. crispa + Salix spp.
11. A. rugosa + Salix spp.
12. Pinus banksiana Lambert (only at St-Louis and Amos)
13. A. crispa + P. banksiana (only at St-Louis and Amos)
14. A. rugosa + P. banksiana (only at St-Louis and Amos)
15. Control (weeds controlled)
16. Control (weeds untreated)
17. Populus balsamifera L.
18. A. glutinosa + P. balsamifera
19. A. glutinosa

Not all the treatments were used on all sites. For example, Pinus banksiana was only planted at St-Louis and Amos, where it replaced the balsam poplar (Populus balsamifera). The number of treatments used was affected by the availability of plants. All treatments were replicated twice in each plot and allocated to sub-plots at random within the plots. More details are given in Fortin (1981 a and b).

Table 1: Location and characteristics of the experimental plantations[1]

Region	Location	Site[2]
1- Quebec	St Lambert	Poorly drained heavy loam soil on an agricultural site
1- Quebec	St Lambert	Peat bog
1- Quebec	Villeroy	Well drained sandy soil
2- Temiscouata	St Louis	Loam, previously a farm
3- Abitibi	Amos	Abandoned agricultural soil, gradient from well drained sandy soil to poorly drained clay loam

[1] More details in Fortin (1982)
[2] All sites ploughed and harrowed after removing forest regeneration

Table 2: Species, propagation, and provenance

Species	Method of propagation	Provenance
Populus tremuloides	Seeded	Laval University (Lots DF, 61) East Angus (Lots By, C)
Populus balsamifera	Cuttings	Laval University
Populus x hybrid	Cuttings	Ministry of Energy & Resources Duchesnay (M52, M53 USA)
Alnus crispa	Seed	Manicouagan River (Manic 5)
Alnus rugosa	Seed	Cap-Rouge (Lot 141) Rivière aux Castors
Alnus glutinosa	Wild	Arboretum at Villeroy
Salix alba	Cuttings	Ministry of Energy & Resources (5012, 5020, 5022, 5023)
Salix nigra	Cuttings	Ministry of Energy & Resources (5012, 5013, 5015)
Pinus banksiana	Seed	Provincial nursery, Ste-Modeste (2-0)

2.3 Site calibration

Physical and chemical analyses of the soil were carried out and the results are summarized in Tables 3 and 4. More details are available in the earlier reports by Fortin (1981a and 1981b). The proportions of different soil particle sizes were measured by densimetry, the organic carbon by dichromate oxidation, total nitrogen by macro-Kjeldahl, available phosphorus by Truog's reagent, and exchangeable cations and cation exchange capacity by 1N ammonium acetate at pH 7.0.

Table 3 shows soil particle sizes for each site. The St-Lambert, Villeroy, and St-Louis sites were all relatively uniform in contrast to the variable Amos soils. Table 4 gives the chemical characteristics and cation exchange capacities of the sites.

The sites were very different, as was expected. It was clear that the two soils at Amos, sandy and clay, have distinct characteristics and this reduced the value of the site for experimental purposes. The levels of calcium and magnesium in the peat bog show that it was dressed with dolomite (Ca + Mg) in the past.

2.4 Survival

After one year the survival of trees on the plots was assessed and it was clear that in some plots there was appreciable mortality (Table 5a). Losses of trembling aspen were surprisingly high (16% to 38% near Quebec City and 97% at Amos) and that of alders fairly heavy (18% to 59%). In contrast, hybrid poplar and willow losses were small and jack pine survived well at St-Louis although 63% were lost at Amos.

The heavy loss of aspen was due to a combination of severe attacks by insects and diseases and a late frost at Amos; the diseases will be discussed later. The other losses were due to a variety of factors including weed competition (especially at St-Louis and Amos) frost lift (e.g. at Villeroy), and drainage (e.g. at St-Lambert and Amos). The peat bog at St-Lambert was deficient in some nutrients (e.g. phosphorus) and it may be necessary to fertilize this site to obtain better tree survival. That would interfere with the experiment to some extent.

After one year the Amos and peat bog sites were not promising. Losses were replaced and survival in 1982 was much better (Table 5b). Even so, the Salix failed on the sandy soils of Villeroy.

2.4.1 Pests and diseases (M. Dessureault)

Although Alnus rugosa and the introduced A. glutinosa were free from damage by pests and diseases, locally A. crispa was severely damaged by alder saw fly (Arga macleayi (Leach)). The willows were attacked by the introduced willow leaf beetle (Plagiodera versicolor (Laich)) and the willow flea-beetle (Orchestes rufipes Lec.). Most severely attacked was the trembling aspen, which was unexpected because it grows naturally in the area and has presumably adapted to local pathogens. The aspens were damaged by a combination of willow flea-beetle, numerous aphids, and shoot burn, the latter damaging the new year's shoots. Most aspen were completely defoliated, and heavy mortality or severely reduced growth can be expected.

If trembling aspen fails it will be necessary to replace it with either another provenance or another indigenous poplar species. Chemical control is not likely to reduce these problems.

Table 3: Average physical characteristics of soils in the experiments[1]

Block	Sand %	Coarse silt %	Fine silt %	Clay %	Texture Class[3] %
St-Lambert[4]	45	13	23	18	loam
Villeroy[4]	83	6	5	5	loamy sand
St-Louis[5]	49	12	20	20	loam
Amos[2/6]	65	10	10	15	loam to loamy sand

[1] More details and coefficients of variation are given in Fortin (1982). All values are means of 4 plots per block.
[2] Amos turned out to be a very variable site.
[3] Canadian System of Soil Classification.
[4] n = 8
[5] n = 11
[6] n = 16

Table 4: Mean chemical characteristics of the soils[7]

Site	pH	Organic carbon (%)	Total nitrogen (%)	Cation exchange capacity (meq $100g^{-1}$)	Available[1] phosphorus (ppm)	Exchangeable[1] potassium (ppm)	Exchangeable[1] magnesium (ppm)	Exchangeable[1] calcium (ppm)
St-Lambert[1]	4.9	1.9	0.13	11.0	54	32	72	438
Peat bog[1]	4.7	50.7	1.22	71.8	28	110	273	13842[3]
Villeroy[1]	4.4	2.0	0.10	17.0	80	24	15	111
St-Louis[2]	4.7	4.3	1.9	17.6	94	103	120	92
Amos a)	5.1	1.4	0.07	5.5	53	35	33	546
b)	5.0	2.6	0.11	14.5	88	48	155	1040

[1] Mean of 64 plots
[2] Mean of 96 plots
[3] Previously limed. Magnesium levels also high in the peat bog so there may have been a dolomite (Ca + Mg) dressing in the past
[4] Sandy soil
[5] Clay soil
[6] Details in Fortin 1982

Table 5(a): Mortality one year after planting, Fall 1981

Species	Villeroy[1] no. (%)	St-Lambert[2,3] no. (%)	St-Louis[2] no. (%)	Amos[3,4] no. (%)	Total no.	Comments
Populus tremuloides	115 (16)	271 (38)	282 (26)	1390 (97)	2058	Amos – frosted after planting, spring 1980
Populus balsamifera	*	*	–	–		
Populus X hybrid (M52, M53)	29 (4)	50 (7)	54 (5)	305 (21)	438	
Alnus crispa	368 (41)	394 (44)	960 (59)	**	1722	
Alnus rugosa	195 (22)	322 (36)	480 (30)	**	997	
Alnus glutinosa	264 (49)	97 (18)	–	–	361	
Salix alba	125 (17)	90 (12)	402 (37)	–	617	
Salix nigra	–	–	–	146 (10)	146	
Pinus banksiana	–	–	102 (9)	914 (63)	1016	Small plants used; frost

* Planted in spring 1981 – good recovery with 5% to 10% mortality
** Planted in spring 1981 – *Alnus crispa* recovered well following damage on all sites (5% to 10% mortality)
1 Frost lift occurred on this site
2 Problems of weed control on these sites
3 Drainage problems
4 Late frost

Table 5(b): Number of living trees and % mortality in brackets (for 30 trees maximum per plot), Fall 1982.

	St-Lambert	Villeroy	St-Louis	Amos
PH	115 (4.2)	119 (0.8)	178 (1.1)	192 (20.0)
PT	94 (21.7)	108 (10.0)	150 (16.7)	
PB	91 (24.2)	109 (9.2)		
S	107 (10.8)	68 (43.3)	132 (26.7)	190 (9.5)
PG			170 (5.6)	213 (11.3)
PH-AR	114 (5.0)	116 (3.3)	150 (16.7)	
PH-AC	113 (5.8)	118 (1.7)	177 (1.7)	410 (14.6)
PT-AR	84 (30.0)	112 (6.7)	142 (21.1)	
FT-AC	103 (14.2)	115 (4.2)	145 (19.4)	204 (15.0)*
PB-AG	104 (13.3)	116 (3.3)		
S-AR	98 (18.3)	108 (10.0)	141 (21.7)	
S-AC	95 (20.8)	102 (15.0)	147 (18.3)	410 (14.6)
PG-AR			154 (14.4)	
PG-AC			170 (5.6)	368 (23.3)
AG	117 (2.5)	118 (1.7)		
AR	92 (23.3)	120 (0.0)	153 (15.0)	
AC	82 (31.7)	117 (2.5)	164 (8.9)	414 (13.8)

* For *Alnus crispa* only, *Populus tremuloides* not sampled.

2.4.2 Diseases of alders (Alnus) (G. Tardif)
A literature survey of alder diseases was carried out as spin-off from ENFOR research and a report prepared by G. Tardif (1982) (Table 6). The report lists the diseases of seeds, fruits, flowers, seedlings, leaves, stems, and roots, their English, French, and Latin names, and their importance. The author concludes that the main problems are likely to be white rots of the stems (particularly on moist sites but less so in plantations) and deformation of the female catkins by the fungus Taphrina, which is likely to affect seed production. Many other diseases occur on alders but few appear to be serious. Nevertheless, many Myxomycetes occur on alders in Europe, particularly on Alnus glutinosa (L.) Gaertner and A. incana (L.) Moënch. These eukaryotes are common on tree bark, dead wood, leaves, and decomposing organic matter. Their roles are not understood.

2.4.3 Tree nutrition on the peat bog (G. Beaulieu and G. Pregent)
The problems encountered in the peat bog at St-Lambert had some bearing on the problems of tree establishment in general. Beauleiu and Pregent (1980) examined nutrient levels of the trees and soil and concluded that there were both phosphorus and nitrogen deficiencies.

The peat on the site contained 1.2% nitrogen with a pH of 4.7, but most of the nitrogen (89% to 99%) was in an organic form, and the available phosphorus was only 28.5 ppm, which is very low compared with 52.8 ppm on other mineral soils nearby.

After leaf and soil analyses the authors concluded that phosphorus deficiency on the peat site resulted in a diminution of photosynthesis in the alders. This would reduce the energy available for both mycorrhizal and actinorhizal symbioses, lowering uptake of combined nitrogen and the phosphorus.

2.5 Prediction equations (G. Pregent)
Total heights and diameters of 30 trees per plot were measured in the field, and one tree per plot selected at random for analysis. If the trees had more than one stem the tallest was measured. Diameters were measured at the root collar on trees grown from seed, and above the cutting where trees were established vegetatively. Trees from the buffer zone were broken down into components (leaves, stem + shoots), dried (65°C), weighed, and analysed. A total of 1359 samples were taken for analysis, i.e. 453 leaf samples, 453 stem and shoot samples, and 453 samples of 3rd and 4th leaves of all trees except Salix (5th leaves) and jack pine (current growth). Samples were ground to pass a 20 mesh sieve and analysed for nitrogen (micro-Kjeldahl), phosphorus (vanadomolybdophosphoric yellow + dry ashing + NHCℓ), potassium, magnesium, and calcium (dry ashing and flame emission spectrophotometry).

Several forms of biomass equations were tested (linear, multiple linear, and allometric). Finally, the allometric equation

$$\text{Log } Y = a + b \text{ Log } x$$

where x = either $(\text{diameter})^2 \times \text{height}$ (i.e. D^2H) or D.H

was used because it gave the smallest error mean square of the variants.

Table 6: Diseases of alder (after Tardif 1982)

Armillaria root rot	Leaf spot[10]
Anthracnose[2]	*Melanconis* canker
Brown cubical rot[1]	*Melanconis* dieback
Brown leaf blotch[2]	*Nectria* canker
Butt rot[3]	*Nectria* dieback
Catkin blister[4]	Powdery mildew[11]
Cenangium canker	Silver leaf[4]
Cytospora canker	Stain[12]
Daldinia root rot	Tip blight[13]
Damping-off[5]	*Tremella* canker
Diatrypella canker	Trunk canker[14]
Didymosphaeria canker	Twig blight[15]
Dieback[6]	*Tympanis* canker
Eutypella canker	*Valsaria* dieback
Fomes root rot	White crumbling rot[16]
Godronia canker	White heart rot[17]
Heart rot[7]	White mottled rot[17]
Hypoxylon canker	White rot[17]
Hysterographium canker	White sap rot[16]
Laminated root rot[8]	White spongy rot[16]
Leaf blister[4]	White stringy rot[16]
Leaf curl[4]	White trunk rot[17]
Leaf rust[9]	Wood rot[18]

[1] e.g. *Coniophora*; [2] e.g. *Cercoseptoria*; [3] *Panus torulosis* Fr.; [4] *Taphrina* spp.; [5] *Fusarium oxysporum* Schlecht.; [6] *Cryptospora*, *Valsa*; [7] e.g. *Hericium*, *Pholiota*; [8] e.g. *Phellinus* (syn. *Poria*); [9] *Melampsoridium*; [10] e.g. *Sphaerulina*; [11] e.g. *Microsphaera*; [12] *Chlorociboria*; [13] *Microsphaerella*; [14] *Hymenochaete*; [15] *Melanconium*; [16] e.g. *Stereum* [17] e.g. *Poria*; [18] *Corticum*

The equations to predict biomass and nutrient content of trees are given in the tables of Appendix. These equations will be of value for future prediction of biomass and content of trees as the experiments develop. Biomass and nutrients content of trees in the plots were assessed by these equations for calibration purposes. These data are listed for each site in Appendices II and III.

2.6 Establishment of plots at Laval University Nursery (C. Camiré and R. Camirand)

Laval University placed a 0.55 ha nursery on the campus at the disposal of the Faculty of Forestry in 1980, and ENFOR funded plots were established on the site in 1981. Previously the area had grown hardwoods and the soil is a loam. Some difficulties were encountered in controlling weeds and hand weeding was supplemented by herbicides.

Table 7 lists the ENFOR work done on this site. Some of the area was used to raise plants of Populus, Alnus, Salix, Comptonia, etc. for the experiments described elsewhere in this report, but there were also studies of Alnus glutinosa provenances, competition between poplars and alders, and nutrient cycling.

3.0 THE NUTRIENT CONTENT OF ALDER LITTER SOILS IN STANDS OF ALNUS RUGOSA
(C. Camiré, I. Girard, and C. Godbout)

Although something is known about the soils beneath red alder (Alnus rubra Bong.) and the characteristics of its litter, there is little knowledge of the soil and litter in stands of Alnus rugosa. Consequently, a parallel study of Alnus rugosa var. americana (Regel) Fern. sites was carried out by Girard and Godbout (1980) to obtain preliminary data, while experimental plots at St-Louis, St-Lambert, Villeroy, and Amos were being established. They studied two alder stands near La Guadeloupe and one stand near Courcelles, in the Beauce-Sud Region of the Province of Quebec at 45°59' to 45°52'Lat.N. and 70°58' to 70°54' Longitude W. Most of the surrounding vegetation was coniferous or mixed forest. Mean heights of alders in the three plots were 3.5 m, 6.0 m, and 3.8 m, and the trees were about 16 to 21 years old.

The soil types varied from gleysol (site 1), to a regosol (site 2) and a mesisol on site 3. Drainage varied from poor to moderate, and pH varied with depth of the sample, but at 0 to 10 cm it was about 4.9 to 5.0, similar to that reported for an Alnus rugosa stand on a gley by Gradtner and Lafond (1958).

In these stands the leaves contained 2.2% to 2.3% nitrogen, and about 465 to 870 ppm of phosphorus. Levels of bases in the leaves ranged from 3060 to 5980 ppm for potassium, 2630 to 3950 ppm for magnesium, and 3560 to 5860 ppm for calcium.

In parts of the alder stands there were balsam firs (Abies balsamea (L.) Mill.) and the nutrient contents of leaves of these firs were compared with those of firs grown without alder. In terms of concentrations the alder did not have any marked effect on the nutrient content (Table 8) but leaves of the balsam fir associated with the alder were heavy (458 mg per 100 current year's leaves) compared with fir without alder (288 mg per 100

leaves). Consequently in absolute terms (mg per 100 leaves) the N, P, K, Ca, and Mg contents of the leaves of fir with alder were all higher than those without (Table 9). The nitorgen content of fir leaves, for example, was 8.04 mg per 100 leaves in the alder stand, and 4.41 mg per 100 leaves without alder. These preliminary data indicate the advisability of using absolute values in assessing the impact of alder on other species. The authors found that alder leaf litter fall weighed 1 600 kg ha^{-1} $year^{-1}$ and contributed about 43 kg ha^{-1} year of nitrogen to the soil. They also found in vitro evidence that there was considerable production of mineral nitrogen in Alnus ruqosa humus, and that significant nitrification was observed even at a pH as low as 3.9, suggesting the presence of acidophilic strains of nitrifying bacteria.

4.0 COMPETITION BETWEEN HYBRID POPLAR AND BLACK ALDER (ALNUS GLUTINOSA)

(C. Camiré, B. Côté, and P. Bellefleur)

An experiment was established in the Laval University campus nursery in the spring of 1981 to study the interaction of hybrid (Roxbury) poplar, which are likely to be used in intensive energy plantations, and Alnus glutinosa from Villeroy. The latter was used because, although it is not native to Canada, it has a clearly defined stem and is known to grow well in the conditions of eastern Canada (pers. obs.).

Four tree mixtures (pure alder, 2 alder to 1 poplar, 1 alder to 2 poplar, pure poplar) were used at three different spacings (33 cm, 66 cm, and 99 cm) on 36 5 m x 5 m plots. In 12 plots ceramic tension lysimeters were established. The results are presented on the basis of individual trees kg ha^{-1} (Appendix IV). A parallel greenhouse experiment was also established.

Heights, diameters, and weights of the trees were measured and the nitrogen content of the lysimeters assessed monthly. The data in Appendix IV indicate that when close spacing (33 cm) is used the stems of individual poplar plants are relatively heavy, particularly where two alder plants are used, reflecting the effects of alder and its nitrogen-fixing symbiosis. At the 66 cm spacing the effect of alder on poplar stem weights was less and at the 99 cm spacing the poplar stems tallied in weight with pure poplar plots. The presence of alder (Appendix IV) increased weights of individual stems and stems + leaves on the plots, compared with pure poplar, except at the wider spacings when both alder and poplar grew best on their own. Appendix IV reflects numerous complex individual tree interactions which will be analysed.

When data are examined on total yield per unit area basis (kg ha^{-1}) the trends are much more consistent (Appendix IV). Firstly, the total yields of stems and leaves of both alder and poplar are double or triple that of plots with alder, compared to those of pure poplar. For example (Appendix IV), at the 33 cm spacing the increment on plots of pure poplar were 4060 kg ha^{-1} $year^{-1}$, compared with 8460 kg ha^{-1} $year^{-1}$ in the plot with an alder:poplar ratio of 2:1. These effects persist at the wider spacings. Incidentally, the pure alder stands had considerably higher yields than the pure hybrid poplar in all cases. Similar trends occurred for stem growth.

Table 7: Description of ENFOR funded activities in the Laval University nursery

Researcher	Area size (m)	Activity
1. C. Camiré P. Bellefleur	60 x 36	48 5m x 5m plots of *Populus* hybrids and *Alnus glutinosa* used to study competition and nutrient cycling.
2. J.R. Thibault	10 x 25	Study of the allelopathic effects of *Populus balsamifera* on *Alnus rugosa*.
3. R. Camirand	15 x 10	Planting stock for the field plots at St-Louis, Villeroy, etc. *Alnus rugosa*, *Alnus glutinosa*, *Populus tremuloides*, *Populus* hybrids (M52, M53), and *Salix alba*.
4. R. Camirand	30 x 15 15 x 15	Study of growth and survival of 43 provenances of *Alnus glutinosa*.
5. R. Camirand	30 x 2.5	Raising plants of actinorhizal non-legumes for experimental purposes (e.g. *Comptonia*).
6. Other work not related to ENFOR		*Ulmus americana* L. plants, *Juglans nigra* L., and *Fraxinus* spp., etc.

Table 8: Concentration of nutrients in leaves of *Abies balsamea* with or without alder (after Girard and Godbout 1980).

Site	Age of balsam fir leaves	N %	P ppm	K ppm	Mg ppm	Ca ppm
Alder stand	current year	1.71	925	4960	975	4800
	other	1.48	720	3390	780	7760
Balsam fir stand	current year	1.57	1000	5410	1320	3560
	other	1.42	705	2500	1240	10200

Table 9: Nutrient content (mg) of 100 current year's leaves of *Abies balsamea* with or without *Alnus rugosa*

Site	Mean weight of 100 leaves (mg)	N	P	K	Mg	Ca
				(mg)		
Alder stand	458	8.04	0.46	2.45	0.48	2.43
Balsam Fir stand	288	4.41	0.30	1.63	0.41	1.11

Using the natural abundance ^{15}N technique (Appendix IV) the average nitrogen fixation by alder was found to be 68% of its total nitrogen (c. 80 kg N ha^{-1} in the aerial parts). The excess of mineralization of nitrogen (NO_3^-) was highest in pure alder plots (Appendix IV). The excess of nitrogen released by mineralization increased with the proportion of alder in tree mixtures. This may be due to a smaller uptake of nitrogen by the alder which can supply its needs by nitrogen-fixing symbiosis. The loss of nitrogen by percolation was negligible.

In this experiment, and the greenhouse experiment in Part 5, trees were close enough to compete, and the poplar grew faster with alder present, possibly due to commensalism between the two species rather than direct transfer of nitrogen from alder to poplar. There were no signs of allelopathy, although leachates from poplar leaves and buds are known to reduce nodulation, germination, and growth of alders (see Part 8). On the basis of these results two hypotheses were formulated. Firstly that alder, because of its nitrogen-fixing symbiosis, takes less nitrogen from the soil pool leaving more for the associated poplar i.e. reduces competition for this element. Secondly, the poplar may explore a larger volume of soil than alder, or explore the same soil volume as alder but over a longer growing season. Both phenomena may apply.

The mixed plots of poplar and alder have a yield of about 10 tonnes ha^{-1} after 2 years (5 tonnes ha^{-1} $year^{-1}$) without application of chemical fertilizer and with decreased output of nitrogen from the soil due to biological nitrogen fixation by alder. These mixed alder-poplar plots were more productive than pure poplar and sometimes less productive than pure alder, depending on spacing. The plots will continue to be observed to ascertain whether mixed plots ultimately 'outgrow pure alder, and to observe changes in nitrogen cycling and distribution.

5.0 CYCLING OF NITROGEN IN ALDER IN THE GREENHOUSE
(C. Camiré and B. Côté)

The principal aim of this work was to establish a nitrogen balance sheet for black alder (Alnus glutinosa) and evaluate nitrogen pathways in the alder, the effects of the alder in soil, and the tree's influence on the mineral nutrition of poplar (hybrid poplar and aspen). The field experiment is previously described in Part 4. The present report concerns a parallel greenhouse experiment.

The plants were grown in 16 60 cm x 60 cm plexiglass boxes containing 85 kg of nursery soil. Two ceramic tension lysimeters and 16 trees were established in each box. It was possible to control and monitor air temperature (maximum 30°C, minimum 20°C to 25°C), soil temperature (17°C to 21°C), soil water content (about field capacity) and nutrient input and output.

Treatments consisted of different proportions of Alnus glutinosa (A) and aspen (P), i.e. 2 A:0P; 1A:1P; 0A:2P; 0A:0P. Tree heights, diameters, and weights were measured, and the leaves, stems, and roots analysed for nitrogen. The nitrogen content of the soil was measured at the beginning and end of the experiment, and the NH_4^+, NO_3^-, and organic nitrogen contents of the lysimeter percolates was measured weekly.

No nodulation occurred on the alders, so no symbiotic fixation of nitrogen took place. This negative result is exceptionally useful because non-nodulated alders are rare and of great value in experiments where the symbioses confuse the issues being studied. It also provides a control for studying nitrogen fixation in the field using the ^{15}N natural abundance method. The biomass production is given in Table 10 where it is clear that total production is highest (2x) in both treatments containing alder. Alder on its own was more productive (2x) than aspen on its own. The nitrogen content was far higher (2x to 3x) in the alder plots even though the alders did not nodulate or fix nitrogen (Table 11). Excess of mineralized nitrogen (NO_3^-) in the alder plots was significantly lower (176 mg NO_3^- $week^{-1}$) than in the poplar plots (200 mg NO_3^- $week^{-1}$) and treeless plots (OA:OP) (222 mg NO_3 $week^{-1}$) (Table 12). Because of the variation it was not possible to evaluate denitrification losses.

The excess of nitrogen mineralization over nitrogen uptake by the plants almost invalidates the lysimeter results.

6.0 GROWTH AND SURVIVAL OF DIFFERENT PROVENANCES OF ALNUS GLUTINOSA (L.) GAERTN.

(C. Camiré)

Alnus glutinosa is not native to Canada but it has a wide distribution in Europe and Asia. Some provenances are known to grow well in eastern Canada. An experiment was established to examine the growth and performance of 43 European provenances of Alnus glutinosa in the nursery at Laval University, St-Foy, Quebec. In this location, mean temperatures are 20.5°C for July and -11.2°C for January, and the mean precipitation 131.4 mm for July and 95.9 mm (including snow) for January. Frosts persist to the beginning of May and occurs again in early October, with 201 frost free days.

The details of treatment of seeds and seedlings, and germination capacity, are described by Fortin (1982). The actinomycete inoculant was of the Frankia ACNI^{AG} type.

The provenances are listed in Table 13. Most of the seed came from Europe (e.g. from Dr. H. Weisgerber of the Forschungsinstitut fur Schnellwachsende baumarten in Germany) from both natural and artificial stands, but one provenance (0X03) came from the United States. The provenances included genotypes from the Soviet Union, Poland, Finland, Estonia, Czechoslovakia, Germany, Switzerland, France, Yugoslavia, Norway, Sweden, Denmark, Ireland, and the United States and ranged from latitudes 61°48'N to 41°56'N.

The plants were raised in a greenhouse with 15 hour days, and measured after 11 weeks as a preliminary assessment prior to planting out in shade halls in September and in the experimental plots on 7th October 1981.

Some provenances survived well in the greenhouse, notably 7221, 2811, 2125, 2220, 4723, 2113, 4X55, 2X03, 2X02, 4X53, and 4X18. The heights of seedlings following sowing varied considerably, and the best greenhouse growth was in provenances from mid-Europe (codes 4 and 5 in Table 13), France and Switzerland (code 6), and Yugoslavia (code 7). The trees were planted out in 1982. Unfortunately most of the trees died for reasons that

Table 10: Production of biomass in the greenhouse experiment (individual plant)

Species ratio	Biomass – dry weight (g/plant)											
	Leaf			Stem			Root			Total		
	P	A	AP	P	A	AP	P	A	AP	P	A	AP
2A		2.4a[1]	2.4a		1.4a	1.4a		1.3a	1.3a		5.1a	5.1a
1A 1P	2.9a	1.9a	2.4a	1.8a	1.1a	1.5a	0.6a	1.4a	1.0b	5.3a	4.4a	4.9a
2P	1.4b	–	1.4b	0.7b	–	0.7b	0.2b	–	0.2c	2.3b	–	2.3b

[1] Duncan's test. Different letters indicate significant (0.05) differences.

Table 11: Nitrogen uptake in the greenhouse experiment (individual plant) in mg

Species ratio	Leaf			Stem			Root			Total		
	P	A	AP	P	A	AP	P	A	AP	P	A	AP
2A		90a	90a[1]		16a	16a		14a	14a		120a	120a
1A 1P	107a	63b	85a	19a	11a	15a	5a	14a	9b	131a	88a	109a
2P	38b	–	38b	5b	–	5b	1b	–	1c	44b	–	44b

[1] Duncan's test.

Table 12: Excess nitrogen NO_3^- from lysimeters in the greenhouse experiment

Species ratio	NO_3^- (mg NO_3^-/week)[1]
2A	176a[2]
1A 1P	105a,b
2P	200b
0A 0P	222b

[1] Ammonium (NH_4^+) concentration was very low compared to nitrate (NO_3^-) and presented no particular trend.

[2] Dunn's Test.

Table 13: *Alnus glutinosa* provenances used in the experiment

Provenance[1]	Location	Latitude	Longitude	Elevation (m)
2144	Molde, Norway	62°42'N	7°40'E	20
2612	Turku, Finland	60°25'N	22°15'E	5
2634	Helsinki, Finland	60°22'N	25°02'E	60
2652	Hameenlinna, Finland	60°55'N	24°25'E	100
2673	Ikaalinen, Finland	61°43'N	23°13'E	90
2812	Tartu, Estonia, Soviet Union	58°10'N	27°36'E	50
2813	Tartu, Estonia, Soviet Union	58°10'N	27°36'E	50
5420	Bialowieza, Poland	52°30'N	23°50'E	150
5813	Banska Stiavnika, Czechoslovakia	48°27'N	18°55'E	475
4X56[2]	Baden-Wurttemberg, W. Germany	– –	– –	–
6313	Basel, Switzerland	47°33'N	7°57'E	350
6365	Aarau, Switzerland	47°18'N	8°03'E	455
6513	Luneville, France	48°30'N	6°29'E	240
6523	Nancy, France	48°47'N	6°18'E	225
6531	Nancy, France	48°48'N	6°16'E	240
0X03	Luther, USA	41°56'N	93°52'W	290
7242	Durdevac, Yugoslavia	46°05'N	17°05'E	113
2163	Steinkjer, Norway	64°12'N	12°14'E	50
7213	Zagreb, Yugoslavia	45°49'N	16°01'E	120
7221	Novoselec, Yugoslavia	45°35'N	16°31'E	95
2811	Tartu, Estonia, Soviet Union	58°10'N	27°36'E	50
2125	Oslo, Norway	59°46'N	10°47'E	45
2220	Sakskobing, Denmark	54°45'N	11°30'E	–
1721	Wrexham, U.K.	52°57'N	3°02'W	50
4714	Offenburg, W. Germany	48°30'N	8°00'E	140
4723	Offenburg, W. Germany	48°30'N	8°00'E	140
7234	Durdevac, Yugoslavia	46°05'N	17°05'E	115
5621	Brzesko, Poland	49°50'N	20°10'E	220
1111	Killeshandra, Ireland	54° 'N	7°30'W	60
4713	Offenburg, W. Germany	48°30'N	8°00'E	140
2113	Oslo, Norway	59°40'N	10°47'E	80
6535	Nancy, France	48°48'N	6°16'E	240
4X55[2]	Baden-Wurttemberg, W. Germany	– –	– –	–
2X03	Kristianstad, Sweden	56°02'N	13°57'E	40
2X02	Hassleholm, Sweden	56°07'N	13°50'E	30
4X31[3]		46°50'N	13°35'E	600
4X53	Munich, W. Germany	48° 'N	11° 'E	650
5411	Brzeziny, Poland	51°48'N	19°50'E	168
2912	Riga, Soviet Union	56°44'N	24°09'E	30
4X14[4]		– –	– –	–
5413	Brzeziny, Poland	51°48'N	19°50'E	168
2914	Riga, Soviet Union	56°44'N	24°09'E	20
4X18[4]		– –	– –	–

[1] Seed lot code used by the Department of Forestry, University of Iowa, USA. 1st digit Geographic Region, 2nd digit Geographic Sub-Region (X = artificial stand source)

[2] Plus tree selection in the seed orchards of Ochsenhausen (4X56) and Weilheim (4X55) in western Germany, grafted and planted in an arboretum.

[3] Selected trees in parent tree (scion) orchard.

[4] Plus trees from West German seed orchards (Information from H. Weisgerber, Munich).

are not understood. Some of the northern provenances from the Soviet Union should have been hardy. It is possible that herbicide residues on the site were involved.

7.0 GROWTH OF *ALNUS CRISPA* AND *SALIX* ON SPOIL HEAPS IN REGION LG-2, JAMES BAY, QUEBEC
(C. Camiré)

This work was not funded directly by ENFOR, but is spin-off from ENFOR and reflects the operational use of results from the research on alders and the actinomycete *Frankia*.

The research (Camire 1982) was concerned with the relationships between location, nutrition, and growth of *Alnus crispa* var. *mollis* (Ait.) Pursh, jack pine (*P. banksiana* Lamb.) and willows (*Salix planifolia* Pursh. and *Salix bebbina* Surg.) growing on borrow bits generated by the James Bay hydroelectric development. Careful biometric analysis indicated that northeastern aspects should be avoided as *Alnus crispa* sites, and that the alder preferred moderately level, moderately drained sites, with sandy loams or loamy sands. The levels of phosphorus and magnesium appear to be important. The jack pine did not grow well on fine, homogenous sands, particularly if the pH was greater than 5. The willows preferred sites with a southeasterly aspect, a pH of about 5, and soils consisting of heterogenous materials with a high proportion of fine sand. The levels of phosphorus were important for good growth of the pine and willow but nitrogen appeared to be limiting.

It was clear that the phosphorus supply limited the growth of alders and that selected mycorrhizae able to take up this element from relatively stable soil phosphates will benefit the trees.

It is worthy of note that, in association with the ENFOR work (see Part 9.6) about one million inoculated alders were provided for operational use in the reclamation of sites during hydroelectric development at James Bay, Quebec.

8.0 ALLELOPATHIC RELATIONSHIPS OF ALDERS AND POPLAR
(J.R. Thibault, R. Jobidon, and P. Younger)

All plants in forests compete for light, water, and nutrients. Some obtain a competitive advantage by affecting other plants through the release of compounds (allelochems) such as polyphenols. This is called allelopathy.

There is good evidence that legume nodulation can be inhibited by associated pioneer plants (Rice 1971) and, in work partly funded by ENFOR, Jobidon and Thibault (1981) found that leachates from leaves and buds of *Populus balsamea* inhibited germination of *Alnus crispa* seed and the growth of the seedling radicle and hypocotyl. They noted malformation of root hairs, which suggests that leachates may affect subsequent nodulation and infection by *Frankia*. The authors also found that leachates from balsam fir (*Abies balsamea*) and balsam poplar (*Populus balsamifera*) inhibited nitrification *in vitro* the allelochems in the extracts, preventing oxidation of ammonium ions (Thibault et al. 1982). Leachates can, therefore, profoundly affect microorganisms involved in the nitrogen cycle,

including nitrogen fixation, and at least one poplar species (P. balsamifera) appears to have potent allelochems in its leachates.

Because short-rotation poplar systems are well suited for planting alders to maintain soil fertility and provide additional fibre, it is highly desirable that the effects of poplar leachates on alder nodulation are understood. An ENFOR-funded investigation was carried out by Jobidon and Thibault (1981, 1982) to assess the allelopathic interference between balsam poplar and Alnus crispa.

The alder seeds were collected from the Val d'Or region in Quebec, the poplar leaves harvested in July, the buds in March, and the current year's litter in October. Poplar leaf leachates were obtained by maceration and standing in water; buds and leaf litter were ground in water in a blender. Both solutions were filtered and centrifuged to remove colloids, and four leachate concentrations (2%, 1%, 0.5% and 0.1%) were applied to the alder seedlings grown in nitrogen-free 50/50 vermiculite/Turface on styroblocks in a growth chamber. The alders were inoculated with the Frankia strain ACNI^{AG}, treated with 15 ml of poplar extracts twice a week with distilled water controls over a period of one month, and harvested after two months. The authors found that even at very low concentrations all extacts inhibited alder height growth, root elongation, and dry weight, and reduced foliar nitrogen levels in both nodulated and unnodulated alder seedlings. All extracts reduced both alder nodulation (by about 51%) and acetylene reduction (by 62%), the latter implying lowered nitrogenase activity. The pH of the media did not appear to affect inhibition.

In this experiment the mechanism of inhibition was not clear, but evidence in the literature indicates that allelopathic agents influence the rate of ion upteke (Rice 1979). The lower levels of nitrogen in the nodulated plants are also probably due to interference with nodulation and nitrogenase activity.

The Frankia endophyte penetrates root hairs to initiate nodules, and other ENFOR work by Jobidon and Thibault (1981) indicated malformation of these hairs by balsam poplar leachates, so that it is likely that this would reduce nodulation. Nevertheless, other physiological factors (e.g. decrease in photosynthesis) could be involved. Allelopathic inhibition of nodulation has been observed in several legumes (Rice 1968).

It is of interest to note that nodulated alders were affected less by the poplar leachates than alders without nodules, suggesting that improved nitrogen nutrition could confer this resistance.

Caution is advisable when considering the ecological and silvicultural implications of the allelopathic effects of balsam poplar on alder growth and nodulation. We still need to know the effects of hybrid poplars and environmental factors such as soil water, temperature, soil colloids, etc. However, it is clear that where foresters are considering using alders mixed with other tree species, they should be aware of the possible effects of allelochems. This does not only apply to alders and poplars, because there are instances of Kalmia allelochems affecting roots of black spruce (Picea mariana (L.) Mills.), sugar maple (Acer saccharinum Marshall) affecting yellow birch (Betula alleghaniensis Britton), and trembling aspen (Populus tremuloides Michaux) leaf litter inhibiting growth of herbaceous species (Peterson 1965, Tubbs 1973, Younger et al. 1980). It is likely that allelopathy plans an important role in the competition and succession of forest vegetation.

An extension of this research on allelochemistry is concerned with assessing the allelochemical effects of bud extracts from seedlings of trembling aspen (Populus tremuloides), balsam poplar (P. balsamifera), and hybrid poplar (P. trichocarpa x P. deltoides, P. balsamifera x P. deltoides) on the germination and growth of Alnus glutinosa. All the trees were 3 to 4 years old except trembling aspen which was 5 to 7 years old (Younger pers. comm.).

Bud-bearing branches of the poplars were collected at Villeroy, Quebec in February 1983 and the buds removed and stored at -20°C. Half-sib seedlots of an Alnus glutinosa provenance from West Germany obtained from the University of Iowa were stratified for ten days at 4°C., sterilized by agitation for 10 minutes in 30% H_2O_2, and rinsed well. The seeds were sown in 50/50 v/v vermiculite-Turface in containers, covered with quartz, raised in a growth chamber at 16 hours photoperiod, with 22°C./18°C. day/night temperature, and 80% relative humidity. The two-week-old alder plants were inoculated with the two-week-old Frankia strain ACN1I^{AG} (from Alnus crispa via A. glutinosa). Two grams of bud material were ground in a blender, filtered and centrifuged (for 20 minutes at 16 000xg) weekly, and made into 1%, 0.5%, and 0.1% solutions. Half of the alders were watered with half-strength Crone's solution with nitrogen, and thinned to 10 plants per treatment at three weeks. The bud extracts (15 ml) were applied twice weekly from the fourth to the eighth week, with distilled water controls. The heights of the alder stems, the lengths of their roots, and the pH of the medium was measured, and subsamples assayed for nitrogenase activity by acetylene reduction. All samples were dried (70°C to 80°C), weighed, and the plants assayed for total nitrogen. Seed germination was also studied. The results are still being analysed and this work will continue. The results obtained so far indicate that the nodulated alders have shorter, thinner, and less dense root systems with fewer root hairs than non-nodulated alder.

8.1 Phenolic acids in balsam poplar leachates and their role as allelochems

This work was partly supported by ENFOR. The aim was to identify phenolic acids (potential allelochems) in the leachates of balsam poplar leaves. It was found by chromatography that the leachates contained phenolic acids of the cinnamic and the benzoic series, and the individual compounds are listed in Table 14 (Perradin 1981).

Addition of phenolic acid to Qmod B medium affected the growth and morphological development of Frankia. Seasonal analysis of balsam poplar leaves and buds showed high content of phenolic substances and a distinct seasonal variation pattern. Results are interpreted in relationship with the succession of alders by balsam poplars observed in the field.

Table 14: Phenolic acids in leachates of balsam poplar *Populus balsamifera* (after Perradin 1981)

Cinnamic series	Benzoic series
para coumaric	gallic
meta coumaric	salicylic
caffeic	prorocatechuic
trans-cinnamic	benzoic
ferulic	syringic
chlorogenic	para-hydroxy-benzoic
	gentisic
	ellagic
	vanillic

9.0 ISOLATION OF SUPERIOR *FRANKIA* STRAINS AND THEIR CULTURE, STORAGE, AND INOCULATION
(P. Normand and M. Lalonde)

Actinorhizal symbioses involving *Frankia* have the potential to improve soils and provide additional fibre in intensive forestry systems, but the success of the symbiosis depends on the efficiency of the nitrogen-fixing microorganisms. *Rhizobium*, the symbiont in the *Leguminosae*, is known to be genetically variable, and since *Frankia* occurs in symbioses in several families and has a wide distribution, it is likely to be variable also.

Frankia was identified as the active symbiont in the nitrogen-fixing non-legumes only recently and no pure cultures were available for study before 1978. Since then four methods of obtaining pure cultures have been developed; sucrose density gradient centrifugation, serial dilution, selective incubation, and osmium tetroxide (OsO_4) treatment (Normand et al. 1982), making it possible to collect, isolate, identify, classify, and evaluate different *Frankia* provenances and establish a bank of strains of the organism. The ENFOR-supported work at Laval University was concerned with these activities. The research started in 1981 is described briefly in Fortin (1982). The aim was to identify and culture efficient strains of *Frankia* for future use in intensive forestry.

Isolation and culture techniques have been developed for *Rhizobium*, but *Frankia* poses special problems. *Rhizobium* produces visible colonies on agar after 2 or 3 days but *Frankia* grows much more slowly, with visible colonies appearing in 2 to 3 weeks or longer. These are also likely to be overgrown by any contaminating bacteria. In addition, the actinorhizal host plants usually contain a greater quantity of phenols than legumes and it is necessary to take precautions against the oxidation of phenols, which appear to inhibit the growth of *Frankia* (Normand et al. 1982).

The biochemistry of the rhizobia is well known, but Frankia's biochemistry is little studied and this is a handicap in Frankia research. The rhizobia only require a relatively simple nutrient medium of yeast extract and sugar, but Frankia isolates, even within the single genus Alnus, have diverse nutrient requirements (Normand et al. 1982). The ENFOR research attempted to overcome these obstacles and develop viable techniques that can meet the needs of future forest operations.

9.1 Collection and isolation

In order to establish a collection of Frankia strains, nodules and soils were collected from native Alnus species (e.g. A. viridis, A. glutinosa, and A. serrulata) and native shrubs such as Myrica gale and Shepherdia canadensis. The main focus of the work was the A. rugosa and A. crispa (Table 15).

Using the OsO_4 isolation method of Lalonde et al. (1981) 250 isolates were obtained from 33 provenances of Alnus spp., Myrica gale, and Shepherdia canadensis. Two hundred of these were from Alnus rugosa and Alnus crispa.

9.2 Inoculation and culture

Nodules were obtained from greenhouse alders grown from surface-sterilized (H_2O_2) seeds (Normand and Fortin 1982), from inoculated Frankia-containing soils from the field, from uprooted field plants established in pots in the greenhouse, or from nodule clusters excised in situ. Each provenance consisted of nodule clusters from one plant.

The water-washed, blotted, nodule lobes were immersed in 3% W/V aqueous OsO_4 for 5 to 6 minutes. After three rinses in sterile distilled water and 5 to 125 min. incubation in sterile PVP-PBS (polyvinyl pyrolidone and phosphate buffer solutions), the single lobes were crushed in new PVP-PBS solutions and transferred to 20 x 150 mm tubes containing 14 ml of Qmod B medium with 5 mg L^{-1} of L-α-lecithin. Fifty tubes per provenance were inoculated at 27°C. Details are given by Normand (1982), Lalonde et al. (1981), and Lalonde and Calvert (1979).

After 2-4 weeks, fluffy whitish outgrowths appeared on the blackened nodules and a presumptive identification of the Frankia isolates was made by the 100x objective of a phase or interference microscope (after Lalonde et al. 1981). Ten tubes of pure, presumptive Frankia isolates were selected, sealed with a rubber serum cap and broken up with a syringe and needle. Subcultures were made in fresh Qmod B tubes.

Identification of sporulating (Sp^+) and non-sporulating (Sp^-) types of Frankia was carried out by examination of 12 m thick sections of nodule lobes, stained with cotton blue by bright field and interference contrast optics prior to use of the OsO_4. The subculture technique was modified for some of the Sp^+ isolates by using the top-layer agar method (Quispel and Burggraaf 1981). There was evidence that the Sp^- strain fixed nitrogen more effectively than the Sp^+ strain.

Table 15: List of provenances from which *Frankia* strains were isolated

Acronym	Isolates' letters	Location	Soil type	Site type	Coordinates lat. N	long. W	Source
A. crispa							
ACN3	a,b,..,j	Tadoussac	SS	W	48°10′	69°40′	PY
ACN4	b,c,..,j	Cap-aux-Oies	SL	RS	47°30′	70°15′	ML
ACN5	a,b,..,j	Lac Beauport	SS	RS	47°00′	71°15′	col.
ACN6	a,b,..,j	Gaspé	SS	RS	48°55′	64°35′	col.
ACN7	a,b,..,j	Percé	SL	DA	48°30′	64°10′	col.
ACN8	a,b,c,d	Baie St-Paul	SS	RS	47°25′	70°30′	col.
ACN10	a,b,..,t	Tadoussac	SS	W	48°10′	69°40′	YP
ACN11	a,b,..,s,u	Baie-St-Paul	SS	RS	47°25′	70°30′	col.
ACN12		Petite-Rivière	SS	RS	47°20′	70°35′	col.
ACN13	a,b,..,j	"	SS	RS	47°20′	70°35′	col.
ACN14	a,b,..,j	Tadoussac	SS	W	48°10′	69°40′	col.
TN15^{AC}	a,b,..,e	Ste-Monique	SS	RS	48°45′	71°50′	ML
ACP17	a,b,..,j	Breakeyville	CL	DD	46°40′	71°15′	col.
TN18^{AC}	a,b,..,h	Manitounuk	SS	W	55°40′	77°25′	AF
ACN20	a,b,..,j	Ste-Louise des-aulnaies	SS	RS	47°15′	70°05′	col.
ACN21	a,b,..,j	Port-au-persil	SS	RS	47°50′	69°50′	YP
A. rugosa							
ARgN4	a,b,..,j	Pointe-à la-garde	SS	DA	48°05′	67°25′	LS
ARgP5^{AG}		Quebec City	SL	RS	46°45′	71°25′	col.
ARgP6	a,b,c,d	Tadoussac	CL	DD	48°10′	69°40′	col.
ARgN8	a,b,..,j	Sherbrooke	CL	DD	45°25′	71°55′	col.
ARgN9	a,b,..,e	St-Calixte	CL	RS	45°55′	73°50′	YP
ARgP12	a,b	St-Samuel	SS	RS	46°05′	72°15′	ML
ARgN14	a,b,..,j	St-Pierre	CL	W	46°15′	71°35′	ML
ARgN/P18	a-c(P) d-f(N)	Grand-Mère	SS	DA	46°35′	72°40′	ML
ARgN22	a,b,..,j	St-Magloire	SS	RS	46°35′	70°15′	ML
ARgN25	a,b,..,j	St-Omer	SS	RS	47°05′	69°40′	ML
ARgN30	a,b,c	Albanel	CL	DD	48°50′	72°20′	JD
A. viridis							
AVP3	a,b,p	Col du corbier (Alpes)	SS	RS	46°	4°(E)	AM
A. serrulata							
ASP4	a,b,..,e	Gainesville Fl. USA	CL	DD	29°	83°(W)	RJ
A. glutinosa							
AGP8	a,b,c,d	Vallée de l'orge (Paris)	CL	DD	49°	2°(E)	JM

Table 15: continued

Acronym	Isolates' letters	Location	Soil type	Site type	Coordinates lat. N	Coordinates long. W	Source
M. gale							
MGP10	a,b,..,j	Cap-aux-Oies	CL	W	47°30′	70°15′	ML
S. canadensis							
SCN9	a	Percé	SL	DA	48°30′	64°10′	col.
SCN10	a	Cap-aux-Oies	CL	W	47°30′	70°15′	ML

The isolate letters give the number of isolate for each provenance; in the case of ARgN18 the Sp^+ isolates are a,b,c and for Sp^- they are d,e,f. The soil type was determined by hand (SS: sandy soil; SL: sandy loam; CL: clay loam). The site types are roadside (RS), wild area (W), disturbed area (DA), drainage ditch or river bank (DD). The sources are P. Younger (PY), Dr. M. Lalonde (ML), Y. Perradin (YP), Dr. J.-A. Fortin (AF), L. St-Laurent (LS), Dr. J. Dawson (JD), Dr. A. Moiroud (AM), R. Iobidon (RJ), and Dr. J. Mugnier (JM).

9.3 Infectivity

Infectivity tests were carried out in plastic growth pouches. Five to ten alder seeds that had been surface sterilized with 30% H_2O_2 + Tween 20 for 5 to 20 min. were placed in the neck of the pastic pouches containing 15 ml of nitrogen-free Crone's solution, and cultured in growth chambers at 15 000 lux for 15 hours and a temperature of 22°/17°C (day/night) until germination. When root hairs appeared, a drop of fragmented Frankia isolate washed in PBS was applied (Normand et al. 1982).

9.4 Effectivity

Lalonde and Calvert's (1979) method was used to assess effectivity in styroblocks. Alder seeds were soaked in cold (2°C) water for three to four days, surface sterilized, and grown in Turface-filled styroblock cavities fertilized with nitrogen-free Crone's solution and germinated under transparent plastic in the growth chambers described above. Some of the nitrogen-starved seedlings were inoculated with the Frankia isolate, and uninoculated controls were kept for each isolate studied. The plants were analyzed after three months for height, weight, and nitrogen concentration to assess the quantity of nitrogen fixed by each isolate. At the same time the three-month-old seedlings were exposed to acetylene reduction assays to assess nitrogenase activity.

These techniques permitted the isolation in pure culture of 250 Frankia strains for addition to the bank of Frankia isolates at the Faculty of Forestry at Laval University (J.A. Fortin and M. Lalonde). This is probably the largest Frankia collection in the world and now contains more than 1000 isolates.

The evolution of the nitrogen-fixing activity of Frankia strains indicated that when Alnus crispa is inoculated with the sporulating (Sp^+) Frankia type, nitrogen-fixation is less efficient than when non-sporulating (Sp^-) Frankia are used. The origin of the host plant from which the isolates were taken did not have a significant effect on nitrogen-fixing

efficiency, but differences were sometimes found between isolates of the same provenance. The sporulating (Sp^+) and non-sporulating (Sp^-) types were so distinct that it was proposed that Type P and Type N need be used to designate the Sp^+ and Sp^- types respectively, and that the sporulation type be used for species definition in the genus Frankia.

9.5 Chromatographic analysis of sugars to identify FRANKIA strains
(P. Normand, J.A. Fortin, and M. Lalonde)

The taxonomy of Frankia can be based on morphology (e.g. sporulation) or infectivity, but it was found that gas-liquid chromatographic analysis of sugars in whole cell hydrolysates of presumptive Frankia isolates is a useful method of supporting or rejecting the identification. Details of the analysis are given in Normand et al. 1982.

Frankia cells were found to contain a spectrum of eight sugars i.e. rhamnose, xylose, 2-O-methyl-D-mannose, galactose, glucose, and inositol. The 2-O-methyl-D-mannose was not found in other actinomycete genera tested (Nocardia, Streptomyces, Actinoplanes) but occurred in all of the Frankia isolates tested. It can only be used tentatively as a Frankia marker, because more work may reveal the sugar in other bacteria. The total Frankia sugar spectrum is suggested as a better isolate identification method (Normand et al. 1982, Mort and Lalonde 1981).

9.6 FRANKIA production and mass inoculation
(J.A. Fortin, M. Lalonde)

The success of the research on isolation, identification, and evaluation of Frankia permitted a first-in-the-world event, namely the industrial scale production of inoculum and its operational use on large numbers of alder seedlings prior to out-planting. The Societe d'Energie de la Baie James (SEBJ) provided 1 000 000 plants for Laval University to inoculate. The C.F. Kettering Foundation at Yellow Springs, Ohio, also participated in the project.

It is preferable to use industrial fermenters to culture the inoculum on a large scale, but such an instrument was not available, and the Frankia was grown in 20 x 150 mm Kim-raks Kim caps test tubes, disposable kits produced by Kimble products. Each tube contained 15 ml of Qmod B medium containing 5 mg L^{-1} of α-lecithin (after Lalonde and Calvert 1979). A 3-week-old actively growing Frankia colony (strain $ACNI^{AG}$) was used to inoculate 50 such tubes.

Sufficient Frankia to inoculate 3 of the medium was taken from test tubes using a Vacutainer blood sampler, and was transferred several times with a syringe (21G needle) to break up the sporangia and liberate the spores. The spores and hyphae were poured into 3 of medium and magnetically stirred, and medium containing spores and hyphae was transferred with a sterile pipette to about 200 autoclaved 15 ml tubes. Inoculation was at 25 $\pm$ 3°C for 4 to 6 weeks, and the colonies grew in the bottom of the tubes. Numerous sporangia were produced.

For small scale inoculation the colonies were collected with a pipette or a Vacutainer-equipped syringe, but for the large scale industrial inoculation, high speed (20 000xg) continuous flow (75 to 100 ml min^{-1}) centrifugation was used. The colonies collected in the bottom of the

centrifuge tubes and were suspended in PBS-PVP buffer or in Crone's nitrogen-free solution and recentrifuged to separate the colonies from the organic components of the Qmod B medium.

The sporangia membranes were broken to release the Frankia spores by passing the inoculum through a narrow syringe under pressure for small scale work, or by using a Virtis blender for larger scale work. The inoculum was kept in 4°C for not more than 4 hours before applying to the alder plants.

The advantage of Frankia inocula is that they can be distributed by standard greenhouse watering devices from which the filters have been removed. Rhizobium has to be applied as slurries to plant roots or seeds. The suspension of Frankia inoculum was kept stirred as the greenhouse irrigation pump slowly distributed the liquid over the 7 to 21-day-old alder seedlings; rapid watering causes losses of inoculum. It requires about one Frankia colony (1 tube) to inoculate 50 alder seedlings. The inoculated plants were fed with nitrogen-free Crone's solution and the technique was entirely successful.

This work clearly demonstrated that mass culture and inoculation of alders and other actinorhizal trees and shrubs with selected Frankia is practical in normal forestry greenhouse practice. The techniques are described in detail in Normand et al. (1982), Fortin (1981) and Fortin (1982), and there is a Frankia bank available at the Faculty of Forestry at Laval University (J.A. Fortin and M. Lalonde). A fermenter is necessary to produce inoculum for 100 000 or more seedlings. The work has moved from basic research to the applied technology and is ready for foresters to use.

This work on Frankia is already being used in the private sector. Les Laboratoires Rhizotec Inc., Ste-Jean-Chrysostôme, P.Q., is already producing Frankia inocula on a commercial basis and there are export possibilities.

9.7 Survival of selected FRANKIA symbionts in the field (M. Lalonde and D.M. Burgess)

When plants are inoculated with selected bacterial symbionts there is always the chance that a selected strain will not be able to compete, survive, and persist against other microorganisms. Many agricultural legumes are annuals or biennials, and the nitrogen-fixing Rhizobium only needs to persist in the plants for one or two seasons. The nodules formed by the selected rhizobia are generally annual but they may persist a second year, sometimes partly suberized. If roots are left in the ground they will decompose and release the Rhizobia into the soil, their job done as far as the annual plant is concerned. The survival and persistence of free-living selected Rhizobia released from the nodules is a point in question and depends on many factors.

Little is known about the persistence of selected Frankia in the nodules of actinorhizal non-legumes, but it can be hypothesized that because these host plants are all perennials and form perennial nodules that can grow to great size (e.g. in alders), the microbial symbiont within the nodules will last longer than in more ephemeral nodules in annual agricultural legumes. The persistence of rhizobia in perennial, arborescent, and shrubby legumes (which have been studied much less than the annuals) is also a point in question. It seems likely that their

nodules will be perennial and the rhizobia relatively enduring. The effect of selected Frankia strains should, at least theoretically, persist over long periods although the possibility that the strain changes within a nodule has yet to be examined.

A part of the Laval University work on nitrogen fixation was to examine the survival of selected Frankia symbionts in the field. A joint experiment between Dr. M. Lalonde of Laval University Quebec, and Mr. D.M. Burgess of the Petawawa National Forestry Institute (PNFI), Chalk River, Ontario, was initiated with three objectives:

(a) To establish a bank of tree species capable of forming nitrogen fixing symbioses with Frankia and examine their survival in the Great Lakes-St. Lawrence Forest Region at Chalk River, Ontario.
(b) To use the survivors to provide a source of vegetative propagules for research and subsequent operational use.
(c) To assess the survival of selected Frankia symbioses in field conditions.

The silvicultural aspects were the responsibility of Mr. Burgess and the culture and selection of the Frankia and the inoculation technique was handled by Dr. Lalonde.

9.7.1 Tree and shrub species

The first phase of the work was concerned with alders and Elaeagnus species. In 1981-82 seeds of 10 alder species and two Elaeagnus were sown in the greenhouse at PNFI in a nitrogen-free medium. After germination half the plants were inoculated with Frankia cultures from Laval University, and half were left untreated as controls. The species and provenances are described in Table 16 and 17. All plants were watered with a nitrogen-free nutrient solution.

9.7.2 Frankia inoculation

Four Frankia inoculants were used from the Laval University bank, two for alder ($ACNI^{AG}$ from Alnus crispa via A. glutinosa and $ACNI^{AG}$ from A. glutinosa), and two for the Elaeagnus (EANIpec from Elaeagnus angustifolia and $EUNI_fS20$, which included an antibiotic marker for Streptomyces, from E. umbellata) (Table 18). All strains were cultivated in March 1981 in Qmod B nutrient medium and transported to PNFI in 24 Vacutainer tubes. At the PNFI laboratory eacn Frankia colony in its Vacutainer was broken up with a 3 ml syringe and a 21 G needle and flushed 10 times or more. The spores and filaments of the $ACNI^{AG}$ and $AGNI^{AG}$ colonies were resuspended in 95 ml of N-free mineral solution and used in watering the plants. Each alder seedling was supplied with 2 ml of solution. The $EUNI_fS20$ and EANIpec cultures were suspended in 45 ml of solution and applied. Each tube inoculated either 50 alders or 25 Elaeagnus.

9.7.3 Performance

The results of this preliminary 1981 trial are given in Table 19. For reasons that are not clear all Elaeagnus inoculations failed. It was decided to repeat this part of the work the following year by inoculating

Table 16: The *Alnus* and *Elaeagnus* species used in the experiment

Species
Alnus cremastogyne Burk.
A. crispa (Ait.) Pursh. (American green alder)
A. glutinosa (L.) Gaertn. (black alder)
A. hirsuta Spach. Ruprecht.
A. incana (L.) Moench (grey alder)
A. japonica (Thumb.) Steud. (Japanese) alder)
A. rubra Bong (red alder)
A. rugosa (Du Roi) Spreng. (speckled alder)
A. sinuata (Reg.) Rydb. (Sitka alder)
A. viridis (DC.) (European green alder)
Elaeagnus angustifolia (Russian olive)
E. commutata (snowberry)

Table 17: Provenances of *Alnus* and *Elaeagnus*

Species	Origin		
	Site	Latitude	Longitude
Alnus crispa	Chapeau, Ont.	47°N	83°W
A. cremastogyne	China	29°N	104°E
A. glutinosa	Penzenskoi Oblast, USSR	53°N	43°E
A. hirsuta	Scotland	(56°N)	(4°W)
A. incana	Eganville, Ont.	45°N	77°W
A. japonica	Perthshire, Scotland	(56°N)	(3°W)
A. rubra	Forbidden Plateau, B.C.	49°N	125°W
A. sinuata	Prince Rupert, B.C.	54°N	126°W
A. rugosa	PNFI Chalk River, Ont.	45°N	77°W
A. viridis	Perthshire, Scotland	(56°N)	(3°W)
Elaeagnus angustifolia	North Dakota, USA	(46°N)	(100°W)
E. commutata	Saskatchewan	–	–

( ) = approximate

Table 18: Provenance of *Frankia* strains

Strain	Original source	
	Species	Location
ACNI^{AG}	*Alnus crispa*	Tadoussac, Quebec
AGNI^{AG}	*Alnus glutinosa*	Netherlands
EANIpec	*Elaeagnus angustifolia*	Ohio
EUNIfS20	*Elaeagnus umbellata*	Illinois

Table 19: Alder seedling inventory – Petawawa National Forestry Institute, summer 1981

Species	Control		Inoculum ACNI[2]		Inoculum AGNI[2]	
	No. of seedlings	Average ht. cm	No. of seedlings	Average ht. cm	No. of seedlings	Average ht. cm
1. *Alnus cremastogyne*	32	16.2	15	20.8	16	18.1
Alnus cremastogyne	186	19.8				
2. *Alnus crispa*	30	6.7	16	8.4	15	9.9
Alnus crispa	149	4.5				
3. *Alnus glutinosa*	44	16.2	16	14.1	24	19.0
Alnus glutinosa	62	20.7				
Extra control	12	19.3				
4. *Alnus hirsuta*	1	9.5	0	0	0	0
Alnus hirsuta	0	0				
5. *Alnus incana*	31	13.8	15	13.9	17	15.6
Alnus incana	279	15.6				
Extra control	3	5.0				
6. *Alnus japonica*	32	13.8	16	18.4	16	15.9
Alnus japonica	193	26.8				
7. *Alnus rubra*	30	9.4	16	11.9	16	14.3
Alnus rubra	170	22.3				
Extra control	1	14.5				
8. *Alnus rugosa*	23	10.0	16	10.6	6	12.2
Alnus rugosa	167	16.9				
Extra control & AGNI	10	9.9			1	3.5
9. *Alnus sinuata*	12	4.2	5	4.1	6	4.1
Alnus sinuata	137	7.7				
Extra control and ACNI and AGNI	13	5.0	2	3.2	10	8.6
No tag (planted same as AGNI)					7[1]	1.8[1]
10. *Alnus viridis*	5	3.2	6	4.2	6	4.2
Alnus viridis	30	3.8				
Extra control ACNI and AGNI			8	1.6	7	6.0

[1] Not confirmed as AGNI

[2] All alder seeds that germinated were successfully inoculated and the plant survived.

host plants at Laval University, where the Frankia bank is located, and transporting them with their nodules to PNFI.

The inoculation success and survival of alders in the first year was variable. None of the Alnus hirsuta inoculations succeeded. Inoculation success was also low in A. sinuata and A. viridis.

The trees and shrubs were planted on a forest soil and their performance will be assessed later. This early trial was only moderately successful in providing research material, and was supplemented in 1982.

9.7.4 The 1982 experiment

A new set of Elaeagnus plants were raised in containers and inoculated at Laval and deliverd to PNFI on 18 May 1982. They included four separate seedlots of E. angustifolia with 28 to 98 plants, and 49 plants of E. commutata. All were inoculated with the selected Frankia strain EUN1$_f$20 (i.e. a strain collected from Elaeagnus umbellata). The container plants were kept in a greenhouse until planting out in nursery beds in June 1982. The fall field survival was 90%, in contrast to the complete failure of 1981.

It is still too early to expect results on alder and Elaeagnus survival and the persistence of the selected Frankia in the perennial nodules on alder and Elaeagnus. The experimental material is in situ and the work will be carried on by Canadian Forestry Service staff in cooperation with Laval University. The strain with the specific antibiotic marker makes it possible to sample the nodules after a few years and find out whether or not the identifiable, selected Frankia and Elaeagnus strains have been replaced by wild types. Although there were problems with Elaeagnus survivals in the first year, these were overcome, and it was clear that the inoculation techniques used were effective. Recent work by Lalonde et al. (pers. comm.) indicates that the plasmid characteristics of the Frankia strains used in this work can be used as a marker in addition to antibiotic resistance.

10.0 RELATIONSHIPS BETWEEN ACTINORHIZAL SYMBIOSES, MYCORRHIZAE, AND THE RHIZOSPHERE

(C. Godbout, M. Couture, B. Côté, J.A. Fortin)

The complex relationships between alder symbioses, mycorrhizae, and free-living soil organisms were described in Part I of this report. In brief, alders have on their roots the nodules of Frankia symbioses, ectomycorrhizae with their fungal sheaths, and Hartig nets in the outer root tissue. In some cases, endomycorrhizae are found deeper in the root tissues. The endo- and ectomycorrhizae send out hyphae into the soil and can tap soluble phosphorus that otherwise would remain out of reach of the trees, thus improving its phosphorus nutrition. Both the mycorrhizae confer other advantages such as energy reserves, resistance to water stress, and possible resistance to root diseases. They are also involved in plant processes in ways that are not fully understood (Fortin and Carlisle 1983). These triple symbioses are unlikely to act in isolation, and any interaction will involve four participants; the host plant (e.g. alder), the nitrogen-fixing actinomycete Frankia, the ectomycorrhizal fungal symbiont, and the endomycorrhizal fungus. These interactions are

complex and are further complicated by the activities of free-living and associative bacteria, fungi (including pathogens), and organisms of the macro- and mesobiota in plant rhizospheres. The rhizospheres contain nutrient-rich conditions due to exudations, root litter, and substrates formed by the death and decay of the numerous organisms in the vicinity of fine roots.

There can be little doubt that the mycorrhizae on actinorhizal non-legumes play a role in providing phosphorus for the ATP energy source of the nitrogenase nitrogen reduction process. Mycorrhizae are linked to the roots of actinorhizae and form hyphal webs in forest ecosystems, and it is possible that they are involved in the distribution of combined nitrogen fixed by actinorhizal plants to other parts of the forest. It is also possible that trees without nitrogen-fixing symbioses possess mycorrhizae in common with alders. This would permit direct transfer of fixed nitrogen from a nitrogen-fixing symbiosis on, for example, the roots of alder to the root tissues of trees without nitrogen-fixing symbioses.

Not much is known about the mycorrhizae of actinorhizal non-legumes, and virtually nothing is known of the role of mycorrhizae in combined nitrogen transport. Before the role of mycorrhizae in nitrogen transfer from actinorhizae to other trees can be examined it is necessary to find out which fungi form mycorrhizae with actinorhizal plants, which of these fungi form mycorrhizae with other forest trees, and whether or not there is evidence of nitrogen transfer.

There is some evidence in the literature (see Part I) that non-symbiotic nitrogen fixation can be considerable in some forest ecosystems and that the activity of free-living or associative bacteria in the rhizosphere may be responsible for nitrogen accretion. A part of the Laval research was to make a preliminary examination of nitrogen fixation in the rhizosphere.

The methods for some of this research have not yet been fully developed, since Frankia was only recently identified as the diazotrophic endophyte in actinorhizae. It is anticipated that definitive answers to questions about the role of mycorrhizal hyphae in nitrogen transfer and the fixation of nitrogen in the rhizophere might not be attained at Laval University with the contract period. Nevertheless, the basic studies completed there would provide information on the suitability of techniques used and provide some insights for future development. All the basic research on actinorhizae and their interactions with the soil micro- and mesobiota is very much at the frontier of knowledge.

10.1 Ectomycorrhizae of alder (C. Godbout and J.A. Fortin)

The aim of this work was threefold. Firstly, to find out which fungi form ectomycorrhizae on alder roots. Secondly, to identify fungi which appear to be superior symbionts with well developed extramatrical fungal sheaths and Hartig nets. Thirdly, to observe whether or not fungi forming alder ectomycorrhizae (that could form a fixed nitrogen pathway) on other tree species such as poplars (Populus) and willows (Salix). The definition of ecto- and endomycorrhizae, their biology, and occurrence on the roots of forest trees are discussed in Fortin and Carlisle (1983).

During the 1980 to 1981 period, 46 pure cultures from 28 potentially mycorrhizal fungi associated with Salix, Alnus, Amelanchier, Betula, Picea glauca, Populus balsamea, P. tremuloides, Pinus resinosa and Abies balsamea

were collected and successfully cultivated. This was extended by further collections, in 1981 to 1982, to 86 strains of 67 different potentially ectomycorrhizal fungi (Table 20), and species of Alpova, Amanita, Cenococcum, Cystoderma, Laccaria, Pisolithus, and Thelephora were obtained from other sources (Fortin and Perinet 1981). Not all these fungi grew well as isolates on agar, but 40 isolates proved to be suitable for experimental synthesis of ectomycorrhizae in plastic growth pouches (Fortin 1981, Godbout and Fortin 1983).

The growth pouch technique is a non-aseptic method to synthesize ectomycorrhizae. It permits a large number of simultaneous tests in a small space in a controlled environment cabinet (Piché and Fortin 1982, Fortin et al. 1983). Other methods, such as using expanded mica (with or without peat moss to counteract the high buffering capacity of the mica) in cotton-stoppered one liter flasks, have been widely used for 20 years. However, in the flasks temperatures can increase, CO_2 can be limiting after a few hours of active photosynthesis by the green plant, it is necessary to add glucose, and results are sometimes difficult to interpret. Methods were developed to overcome these problems, but they are all cumbersome and do not permit observation of ectomycorrhizae genesis and development of the extramatrical phase.

The pouch method involves a flat polyester pouch, with an open neck, containing a thin paper pad and a nutrient solution. The pouch can be clipped shut and hung on a rack in a growth cabinet. The root system of the higher plant grows in one plane on the pad's surface.

In the ENFOR work alder seeds were stratified for two weeks in distilled water at 4°C and germinated on moist silica. After five days the small seedlings were transferred to growth pouches containing 15 ml nutrient solution (modified Crone's mineral solution) leaving the green cotyledons outside the bag. Seven days after the transfer, alder seedlings were inoculated with pure Frankia strain $ACNI^{AG}$. After the formation of visible nodules, between the 45th and 70th day after transfer to pouches, the seedlings were inoculated with ectomycorrhizae. The fungi were grown on MNM agar and introduced into the pouches as plugs, with air spaces maintained between paper and plastic of the pouch by 20x5x5 mm foam. The pouches were closed with clips. Five replicates were made for each host-fungus combination, with uninoculated controls, and the seedlings were raised in pouches in growth chambers under 16 hours of light at 10k lux and a temperature of 22°C/16°C (day/night). Details of the methods are described by Godbout and Fortin (1983).

The success of synthesis of ectomycorrhizae on Alnus rugosa, A. crispa, and Populus tremuloides is given in Table 20. Other authors (e.g. Molina 1979, 1981) have suggested that the genus Alnus may be very specialized in its ectomycorrhizal fungi associates. The ENFOR research indicates that Alnus rugosa and A. crispa form ectomycorrhizae with many fungi, and are not particularly specialized (Table 20).

The development of the ectomycorrhizae varied considerably. In some pouches there were more than 15 mycorrhizal alder root tips per plug of inoculant, some had 5 to 15, and others below 5. The extramatrical phases of these ectomycorrhizae have been described in detail by Godbout and Fortin (1983).

It is of interest to note that of these 10 fungal species forming ectomycorrhizae on alder, five also formed ectomycorrhizae on Populus

Table 20: List of the fungal isolates used, isolation year, associated host, and degree of ectomycorrhiza formation of 46 species of fungi tested with *Alnus crispa*, *A. rugosa*, and *Populus tremuloides*

Isolate no.	Fungus species	Year of isolation	Associated host +	*Alnus rugosa*	*Alnus crispa*	*Populus tremuloides*
CG 281"	*Alpova diplophloeus* (Zerrer & Dodge) Trappe & Smith	1981	Alc	+ + +	+ + +	
77 8	*Amanita citrina* S.F. Gray	1977	–	–	–	–
CG 59	*Amanita muscaria* (Fr.) Hooker	1980	Pot	–	–	+
CG 237	*Amanita rubescens* (Fr.) S.F. Gray	1981	Pid	(–)	–	–
CG 236*	*Boletus ornatipes* Pk.	1981	Bep	–	–	(–)
CG 16	*Boletus piperatus* (Fr.)	1980	Pot	(–)	–	(–)
XX 50	*Cenococcum geophilum* Fr.	1967	Pim	–	+	+
DGL 80221E 15*	*Cenococcum geophilum* Fr.	1980	Pim	+	–	–
CG 274*	*Cortinarius alboviolaceus* (Pers. ex Fr.) Fr.	1981	Pot	–	–	–
CG 283*	*Cortinarius hercynicus* (Pers.) n.c.	1981	Alr, Pot	–	–	–
DM 20 8 80/1*	*Cortinarius semisanguineus* (Fr. Gill.	1980	Pim	–	–	–
CG 47*	*Cortinarius* cf. *subporphyropus* (Pilát)	1980	Pot	+ +	+ +	+
77 9	*Fuscoboletinus glandulosus* (Pk) Pomerleau & Smith	1977	Pim	–	–	–
CG 219	*Gautieria graveolens* Vitt.	1981	Pim	(–)	–	–
CG 225	*Gyrodon merulioides* (Schw.) Sing.	1981	Fra	–	–	–
CG 2	*Gyrodon merulioides* (Schw.) Sing.	1980	Fra	–	–	–
CG 205	*Gyromitra esculenta* Fr.	1981	Pim	–	–	–
CG 278*	*Hebeloma crustuliniforme* (Bull. ex St-Amans) Quélet	1981	Pot	+	+	–
75 1	*Hebeloma cylindrosporum* Romagnési	1975	Pip	–	–	–
CG 208*	*Hebeloma mesophaeum* (Pers. ex Fr.) Quélec	1981	Pot, Sa	–	–	+
CG 273*	*Hebeloma* cf. *velutipes* Bruchet	1981	Pot	–	–	–
CG 211	*Laccaria laccata* (Fr.) B. & Br.	1981	Alr, Pot	+	+	+
CG 258*	*Lactarius hibbardae* Pk. var. *hibbardae*	1981	Pot	–	–	–
CG 277*	*Lactarius pubescens* Fr. var. *pubescens*	1981	Bep	–	–	–
CG 53*	*Leccinum aurantiacum* (Bull. ex St-Amans) S.F. Gray	1980	Pot,	–	–	+
CG 22	*Leccinum griseonigrum* Smith, Thiers, & Watling	1980	Pot, Pir	–	–	+
CG 72	*Leccinum holopus* (Rostk.) Watling	1980	Bep	+	+	–
CG 235*	*Leccinum* subglabripes (Pk) Sing.	1981	Bep, Pot	–	(–)	–
CG 242	*Leccinum subglabripes* (Pk) Sing.	1981	Pot, Bep	–	–	–
CG 269*	*Leccinum subleucophaeum* Dick & Snell	1981	Bep	+	+	–
CG 82	*Lycoperdon perlatum* Persoon	1980	Pot	–	–	–
CG 210	*Mutinus caninus* (Pers.) Fr.	1981	Tho	–	–	–
CG 9	*Paxillus involutus* (Batsch.) Fr.	1980	Pot	+ +	+ +	+
76 1	*Pisolithus tinctorius* (Pers.) Coker & Couch	1976	–	+	+	+
CG 77*	*Psathyrella rigidipes* (Peck.) A.H. Smith	1980	Sa	(–)	–	–
CG 218	*Rhizopogon*	1981	Pim, Pid	–	–	–
CG 229	*Rhizopogon*	1981	Pid, Pir	–	–	–
CG 261	*Rhizopogon*	1981	Pir	–	–	–
CG 240*	*Scleroderma arenicola* Zeller	1981	Acs, Fag	(–)	(–)	–
CG 65	*Scleroderma citrinum* Pers.	1980	Alc. Bep	+	+	+
CG 224	*Scleroderma citrinum* Pers.	1981	Fag	–	(–)	–
DGL 81121B*	*Scleroderma citrinum* Pers.	1981	Fag, Qur	–	–	–
CG 241*	*Scleroderma lycoperdoides* Schw.	1981	Acs, Fag	–	(–)	–
77 12	*Suillus grevillei* (Klotzsch) Singer	1977	Lal	–	–	–
77 1	*Suillus tomentosus* (Kauf.) Sing., Snell & Dick	1977	Pid	–	–	–

Table 20: continued

Isolate no	Fungus species	Year of isolation	Associated host +	*Alnus rugosa*	*Alnus crispa*	*Populus tremuloides*
CG 128	*Thelephora terrestris* (Ehrh.) Fr	1980	Pot			+
CG 260	*Tricholoma cingulatum* (Fr.) Jacobasch	1981	Pot, Sa			
CG 41	*Tricholoma falvovirens* (Fr.) Lund	1980	Pot	(-)		(-)
CG 93*	*Tricholoma populinum* sensu Pilát	1980	Pot			+
CG 263*	*Tricholoma sejunctum* (Fr.) Quél.	1981	Pir	(-)		
CG 71*	*Xerocomus subtomentosus* (Fr.) Quél.	1980	Pot			
CG 244*	*Xerocomus subtomentosus* (Fr.) Quél.	1981	Pim			

* Vouchers at the Univ. of Toronto herbarium

+ + + > 15 mycorrhizal root tips per plug, + + between 5 and 15, + below 5 without mycorrhizae formation

(-) no visible growth of the fungi in the pouch

+ Acs: *Acer saccharum* Marsh., Alc: *Alnus crispa* (Ait.) Pursh, Alr: *Alnus rugosa* (Regal) Fern, Bep: *Betula papyrifera* Marsh., Fag: *Fagus grandifolia* Ehrh., Fra: *Fraxinus americana* L., Lal: *Larix laricina* (Du Roi) K. Koch, Pid: *Pinus divaricata* (Ait.) Dumont, Pim: *Picea mariana* (Mill.) B.S.P., Pir: *Pinus resinosa* Ait., Pot: *Populus tremuloides* Michx., Qur: *Quercus rubra* L., Sa: *Salix* sp., Tho: *Thuja occidentalis* L.

tremuloides. These were Cortinarius cf. subporphyropus, Laccaria laccata, Paxillus involutus, Pisolithus tinctorius, and Scleroderma citrinum. Some of the other successful inoculants, such as Hebeloma crustuliniforma and Cenococcum geophilum, are all considered to have a broad range of host species, and some of the fungi listed in Table 20 may well form ectomycorrhizae with alders and other trees under different conditions. The fact that alders have at least some (and possibly many) mycorrhizal symbionts in common with other trees suggests that theoretically it is possible that there is a hyphal nitrogen transfer pathway from trees with nitrogen-fixing symbioses to trees lacking the symbiosis.

At sites where ectomycorrhizae formed on the alders some had a regular Hartig net between the cells of the root's epidermis, some a net only distally, and some no net at all. In Alpova diploploeus there was a well-distributed Hartig net right up to the root cap, but only between epidermal cells and not in the cortex. In other mycorrhizae, such as those formed by Paxillus involutus, the epidermal net was only seen at the base of the mycorrhizae. In some mycorrhizae (e.g. Alpova on Alnus rugosa) the mycorrhizae curved, and the fungus appeared to influence root elongation (Godbout and Fortin 1983).

Although alder can form mycorrhizae with many fungi and is not particularly specific, the genus Alnus appears to be specialized in that only some ectomycorrhizal fungi develop Hartig nets rapidly. The apparently alder-specific Alpova diplophloeus was the only fungus tested that rapidly penetrated between alder root cells to form Hartig nets. Other fungi with a wide range of hosts take longer to adapt, penetrate between the cells, and form a Hartig net. The epidermal Hartig nets observed in the alders (which are in the Betulaceae) differ from the usual

concept of a Hartig net between cells of the cortex. Epidermal nets have been observed in other members of the Betulaceae, such as Betula, Carpinus, and Corylus (Giltrap 1979). In Gymnosperms the Hartig nets usually penetrate several layers into the cortex.

As a result of this work Godbout and Fortin (1983) suggest that there are two distinct types of Hartig net, the cortical net in the Gymnosperms and the epidermal net in the Angiosperms. Which of the two types of Hartig net is most beneficial to the host remains a point in question. The research also indicates that inoculation of an alder root and the formation of nodules does not appear to modify recognition factors nor the internal physiological processes that lead to fungal inoculation and formation of the ectomycorrhizal Hartig net and mantle. This raises many questions about infectivity mechanisms.

10.2 The transfer of nitrogen by alder ectomycorrhizae (M. Couture)

The aim of this preliminary experiment was to ascertain whether or not the actinorhizal alder's mycorrhizae can transport fixed nitrogen via the hypha to a Pinus strobus L. plant with a common mycorrhizal fungus.

Preliminary studies of methods in 1981 to 1982 indicated that multiple pine-alder-Frankia-mycorrhizae symbioses could be created artifically in individual plastic growth pouches described earlier. In the preliminary trials the fungus Pisolithus tinctorius formed mycorrhizae on both alder and pine but favoured the pine, and was replaced by Paxillus involutus. There was an apparent adverse effect of alder on pine roots, possibly by allelopathy, when grown in the same plastic pouch. A twin-pouch technique was devised to overcome this problem (Fortin 1982).

In 1982 and 1983 the twin pouch technique was used with ^{15}N to assess nitrogen fixation by alder, and possible assimilation of fixed nitrogen by pine via mycorrhizal hyphae.

Surface-sterilized seeds were used to raise Pinus strobus and Alnus crispa plants in aseptic conditions. These two species of trees were established in the twin plastic growth pouches and inoculated with Paxillus involutus, which the ENFOR work has shown to form mycorrhizae on alders and other tree species. There were controls without mycorrhizae, and plants were labelled with $^{15}N_2$ at the age of three months.

In order to label the plants with $^{15}N_2$ the isotope was generated from $^{15}NH_4Cl$ (with 99% ^{15}N) by addition of hypobromite. The ^{15}N concentration of the ^{15}N in the N_2 in the atmosphere was estimated as 10%. In order to label the trees, six units of plants were mounted in series and connected to a carbon dioxide trap and a peristaltic pump sealed hermetically by a water manometer. Five coupled plants (one of each species per twin pouch) were used in each of the six units, making a total of thirty plants. Sixteen of these coupled plants were mycorrhizal and 14 were non-mycorrhizal. The whole system was located in a growth chamber with 15 k lux lighting and a temperature of 22°C.

In one experiment the plants were exposed to the labelled $^{15}N_2$ gas for 5 days, and in another for 18 days. The labelled plants were then harvested, divided into stems, leaves, and roots, and dried, weighed, and analysed for total nitrogen by the Kjeldahl process and ^{15}N by mass spectrometry.

The weights, nitrogen content, and ^{15}N fixed are given in Tables 21 and 22. Under the experimental conditions inoculation with mycorrhizae had no significant effect upon the weights of the alder or pine, and this, since the mycorrhizae were only present for three weeks, is to be expected. The alder leaves contained 1.6% nitrogen in the leaves compared with 0.8% in stems and 1.3% in roots. The pine leaves, stem, and roots contained 0.6%, 0.3%, and 0.6% nitrogen respectively.

After five days exposure to $^{15}N_2$ gas the net nitrogen fixation by mycorrhizal alder plants was µ810 gN (162µgN plant^{-1} day^{-1}); 991µg (198µgN plant^{-1} day^{-1}) were fixed by non-mycorrhizal alder. After 18 days exposure to $^{15}N_2$ the mycorrhizal and non-mycorrhizal plants fixed 2626 and 3577µg of N plant^{-1} (150µgN and 200µgN plant^{-1} day^{-1}) respectively. About 50% of the fixed nitrogen was in the roots, 40% in leaves, and 10% in stems.

^{15}N appeared in pine tissues, and the mycorrhizal and non-mycorrhizal pine contained about the same amounts of isotope. The isotope fixation was about 0.5µg^{15}N per plant after five days exposure to $^{15}N_2$ and 2.6µg per plant after 18 days. 90% of the isotope appeared in roots.

Table 21: Weight, nitrogen concentration, and nitrogen fixation of mycorrhizal and non-mycorrhizal alder (*A. crispa*)

	Non-mycorrhizal[1]				Mycorrhizal[2]				^{15}N
	O.D. weight (mg)	N-NH_4 (%)	^{15}N excess (%)	^{15}N fixed mg/plant	O.D. weight (mg)	N-NH_4 (%)	^{15}N excess (%)	^{15}N fixed mg/plant	Natural abundance
Exp. I: 5 days exposure to ^{15}N									
Leaves	244	1.6	0.882	344 (35%)	254	1.6	0.561	288 (28%)	0.0009
Stem	104	0.8	1.451	121 (12%)	115	0.8	1.267	116 (14%)	0.0009
Roots	269	1.3	1.508	526 (53%)	308	1.3	1.168	466 (58%)	0.0046
Total	617			991 (100%)	677			810 (100%)	
mg N fixed per plant per day:				198				162	
Exp. II: 18 days exposure to ^{15}N									
Leaves	369	1.3	1.211	1252 (48%)	434	1.4	2.965	1800 (50%)	0.0034
Stem	147	0.8	2.448	287 (11%)	153	0.8	2.893	354 (10%)	0.0030
Roots	433	1.0	2.518	1087 (41%)	444	1.1	2.916	1423 (40%)	0.0033
Total	949			2626 (100%)	1031			3577 (100%)	
mg N fixed per plant per day:				146				200	

[1] Mean of 14 plants
[2] Mean of 16 plants

Table 22: Weight, nitrogen concentration, and nitrogen fixation of mycorrhizal and non-mycorrhizal pine (*Pinus strobus*)

	Non-mycorrhizal[1]				Mycorrhizal[2]				^{15}N
	O.D. weight (mg)	N-NH_4 (%)	^{15}N excess (%)	^{15}N fixed mg/plant	O.D. weight (mg)	N-NH_4 (%)	^{15}N excess (%)	^{15}N fixed mg/plant	Natural abundance
Exp. I: 5 days exposure to ^{15}N									
Leaves	45	0.6	0.010	0.1 (9%)	58	0.7	0.004	–	0.0065
Stem	16	0.3	0.035	0.1 (9%)	21	0.3	0.016	–	0.0130
Roots	54	0.6	0.030	0.9 (81%)	66	0.7	0.010	0.5 (100%)	0.0021
Total	115			1.1 (100%)	145			0.5 (100%)	
mg N fixed per plant per day:				0.2				0.1	
Exp. II: 18 days exposure to ^{15}N									
Leaves	62	0.6	0.009	0.2 (7%)	63	0.6	0.008	0.2 (8%)	0.0030
Stem	18	0.2	0.044	0.1 (3%)	18	0.2	0.019	0.1 (4%)	0.0035
Roots	70	0 6	0.067	2.6 (90%)	74	0.6	0.057	2.3 (88%)	0.0061
Total	150			2.9 (100%)	155			2.6 (100%)	
mg N fixed per plant per day:				0.2				0.1	

[1] Mean of 14 plants
[2] Mean of 16 plants

The ^{15}N labelling system was successful both for alder and pine. Although the ^{15}N isotope appeared in pine, the differences in ^{15}N content of mycorrhizal and non-mycorrhizal pines were too small to conclude whether or not mycorrhizae were involved in the transfer of fixed ^{15}N from the alder to the pine.

Although the results were inconclusive, it is possible that the mycorrhizae were not sufficiently developed, the period of exposure to $^{15}N_2$ too short, the plants too young, and the method too insensitive. Because alder's root symbioses (Frankia) fix nitrogen and both alder and pine form ectomycorrhizae with Paxillus (and probably other fungi), there does not appear to be any major obstacle to the transfer of nitrogen fixed by alder to the pine. The hypothesis that mycorrhizal hyphae act as a pathway of fixed nitrogen from actinorhizal plants to other plants in the forest ecosystem is worthy of further examination.

10.3 Nitrogen fixation in the rhizosphere (C. Camiré and B. Côté)

The general impression given by the literature is that in the temperate zone free-living microorganisms only contribute relatively small amounts of fixed nitrogen (e.g. 2 to 5 kg ha^{-1} $year^{-1}$) to forest and other soils (Fortin et al. 1983). But on some sites such as grass swards and coniferous forest there are unexplained gains of up to 55 kg ha^{-1}

year^{-1} of soil nitrogen, and it is possible that this is due to non-symbiotic biological nitrogen fixation by free-living and associative bacteria in the rhizospheres of the higher plants (Postgate 1978, Knowles 1965, Fortin et al. 1979, Brouzes et al. 1969). In the tropics, associative bacteria on grasses fix about 5 to 30 kg ha^{-1} year^{-1} and the Azolla-Anabaena association can fix about 60 to 80 kg of nitrogen each year, but no temperate equivalent has been observed.

Nevertheless, it has been observed that grass and grain yields and nitrogen content have been improved by inoculation of the rhizosphere with Azospirillum, a nitrogen-fixing bacterium with wide geographical distribution. This microorganism forms associative symbioses in the mucigel layer (and sometimes the intercellular spaces of the cortex) of roots of plants in the Gramineae. The precise mechanism of the plant-bacteria relationship is not clear. In the laboratory there is some evidence of increased nitrogenase activity of inoculated roots, but it is possible that hormonal balance is involved (Inbal and Feldman 1962).

There is a need to examine the role of these rhizosphere in the field since it has been suggested that they may replace nitrogen fertilizers to some extent in the cultivation of sweet corn (Dobereiner and Day 1976, Avivi and Feldman 1982, Kapulnik et al. 1982). It is interesting to note that this rhizosphere effect is appreciable in sweet corn, a species relatively rich in sugars that could be present in root exudates and provide energy for nitrogenase activity.

It is possible, therefore, that nitrogen fixation in the rhizospheres of trees is more important than is generally thought. ,

A preliminary trial was carried out using cores of hardwood forest soil in a greenhouse planted with alder alone, poplar alone, mixed alder and poplar, and with no trees at all. The alders were a genotype incapable of forming nodules. The cores were located in 15 cm x 3 cm plastic tubes. Acetylene was infested and nitrogenase activity assessed by acetylene reduction assay on a gas chromatograph after 1 hour, 2 hours, and 4 hours. In the first trial only very small amounts of acetylene were reduced, so nitrogen fixation by free-living organisms in the soil and tree rhizospheres was very low. A range of sugars were added in another trial and, although nitrogenase activity was higher than before, it was still low.

Although there was little evidence of nitrogen fixation by free living or associative organisms, it may well be that the method is too insensitive. Better results may be obtained in the future by using ^{15}N isotope tracers and by studying pines rather than hardwoods. This is an area that needs exploration because evidence in the literature suggests that nitrogen fixation by free-living or associative bacteria in the rhizosphere of trees may be greater than is generally thought.

11.0 CONCLUSIONS

11.1 Establishment of plots of alder and other tree species

i The experimental plots of alder and other tree species established at Villeroy, St-Louis, St-Lambert, Amos (Quebec), and the Laval University campus were partly successful in spite of initial

losses from frost, pests, and diseases. It was concluded that, while some attempt should be made to replace losses at Amos and the peat bog site at St-Lambert, future efforts should be concentrated on the loam site at St-Lambert, the Villeroy - St-Louis sites, and the plots on hardwood soil at the Laval University campus.

ii Although the St-Louis, St-Lambert, Villeroy, and Amos sites are still too young to be used for short-term work on the impact of alder on tree growth and soil fertility, these plots, which have been calibrated, will be of considerable value for future research on alder - other tree - soil interactions. This is particularly pertinent to the campus site where there is most control.

iii The mortality of trees on the peat bog was partly due to a phosphorus deficiency which interfered with mycorrhizal and actinorhizal energy supplies, thereby reducing uptake of both nitrogen and phosphorus by these symbioses. This site poses some interesting nutritional problems that would benefit from further examination.

iv The main pests and diseases attacking the trees in the plots were the alder sawfly (Arge macleayi) on Alnus, and the willow leaf beetle (Plagiodera versicolor) and willow flea beetle (Orchestes rufipes) on Salix. The leaf and flea beetles heavily infested Populus tremuloides, which also suffered from aphids and shoot burn. It may be necessary to replace the aspen with another provenance. The sawfly attack on alder led to a survey of alder pests and diseases in general.

v About 46 diseases occur on alders, but the only ones of importance are the white rots of stems caused by such organisms as Poria spp., particularly on moist sites, and the deformation of reproductive catkins by Tephrina, which reduces seed production. The roles of the many Myxomycetes that occur on alder are not understood.

vi Although many insects attack alder, the review of the literature in Part I of this report indicated that the sawflies, particularly introduced sawflies, are likely to be the only major pests on alder. Sawfly damage in the plots reflects this fact.

vii The prediction equations for biomass and nutrients of the relatively small trees in these plots will be of value in future assessments. So far the alders have not affected growth of other species significantly, but it is still too early to say. The soil and trees calibration data are ready for future use.

viii The closely controlled experimental plots which included different combinations of alder and hybrid poplar at different spacings, an Alnus glutinosa provenance trial, and banks of material for studies of allelopathy and nitrogen-fixing actinorhizal plants, are already yielding results and will be of increasing value as research tools in the years ahead.

ix Well designed field experiments to examine the effects of alder on the growth of associated species and on soil fertility are urgently needed on a wide variety of sites.

11.2 Nutrient content of litter and soils on *Alnus rugosa* sites

i The study of natural *Alnus rugosa* stands in Quebec at La Guadeloupe and Courcelles indicated that balsam fir (*Abies balsamea*) associated with alder had higher absolute N, P, K, Ca, and Mg contents than fir without alder. The alder produced about 1600 kg ha^{-1} $year^{-1}$ of leaf litter, equivalent to 43 kg ha^{-1} $year^{-1}$ of nitrogen. *In vitro* the humus of the alder soils produced significant quantities of mineral N and there was sufficient nitrification even at pHs as low as 3.9, suggesting the presence of acidophilic strains of nitrifying bacteria. Studies on natural sites such as these can provide a great deal of information until the main experimental plots become well established.

11.3 Growth of *Alnus* and *Populus* in different mixtures and different spacings

i Preliminary results from the study of effects of spacings and numbers of alders in an alder-poplar stand indicate that, at close spacings, the presence of alders increases poplar growth two to three times after three years. Pure stands of alder had higher yields than pure stands of poplar in all cases.

The distribution and number of alders in a mixed stand is a major determinant of the economic profitability of using alder to increase yield of other trees. Already it is apparent that the number of alders per acre may well vary with the age of the stand. More field experiments are needed to examine this point in order to provide better management guidelines.

11.4 Alder nitrogen budget

i The identification of a rare non-nodulating alder will be exceptionally useful in future experiments with alder where nodulation and symbiotic nitrogen fixation would otherwise obscure other nitrogen processes.

ii The non-nodulating alder identified will provide a control when studying nitrogen fixation in the field using ^{15}N tracer isotopes.

iii Total production and nitrogen content in plots with alder, poplar, and alder + poplar are 2x to 3x higher in plots containing alder.

iv Production and nitrogen content of the poplar increased when alder was present even when the alder did not nodulate and perform symbiotic nitrogen fixation, suggesting commensalism. The reported growth of trees associated with alder may not be simply due to a direct nitrogen effect.

11.5 Growth and survival of *Alnus glutinosa* provenances

i The *Alnus glutinosa* provenance trial in the Laval University nursery had high mortality in 1982-83 for unknown reasons.

11.6 The growth of alder and willow on borrow pits at James Bay, Quebec

i Large areas of disturbed sites at James Bay, Quebec were successfully planted with over one million alder trees in order to demonstrate the operational feasibility of the ENFOR-supported

project at Laval University. The plantings were of alders inoculated with Frankia under research programs funded by other organizations.

ii It was concluded that, at least at James Bay, Alnus crispa should not be planted on slopes with northeasterly aspects. The species prefers moderately level, moderately-drained sites with sandy loams.

iii Suitable phosphorus levels were crucial to good growth of alder and other tree species (Salix spp. and Pinus banksiana) on these sites, and the trees would benefit from inoculation with selected mycorrhizae to facilitate phosphorus uptake.

11.7 Allelopathic relationships

i Extracts from leaves and buds of Populus balsamifera inhibited the growth, foliar nitrogen, nodulation, and nitrogenase activity in Alnus crispa seedlings, and interfered with seed germination.

ii The poplar extracts deformed root hairs which are the sites of Frankia infection of the host. This is probably at least partly responsible for the reduction in nodulation, although interference with photosynthesis may also be a factor.

iii The leachates contained phenolic acids of the cinnamic and benzoic series. They may be the inhibitory compounds.

iv The allelopathic effects of poplar suggest that the influence of companion species on alder in mixed plantations needs to be taken into account when designing stands. More needs to be known about these plant interactions to guide the manager.

v Nodulation of young alder is associated with poorer root development than on alders without nodules.

11.8 Isolation, culture, storage, infectivity and effectivity, and mass production and application of superior strains of Frankia

i Until recently very little was known about Frankia, but the work at Laval University has made it possible to isolate, test, and culture selected strains. This effort has added 250 tested strains of Frankia to the substantial bank of genetic material at Laval; a store of great value in future research and operations involving actinorhizal trees and shrubs.

ii It is clear that there are sporulating (Sp^+) and nonsporulating (Sp^-) strains of Frankia, and that the sporulating type may not be as efficient in fixing nitrogen as the non-sporulating type.

iii The Sp^+ and Sp^- differentiation is regarded as a suitable basis for Frankia taxonomy.

iv Although Frankia is the only actinomycete that contains the 2-O-methyl-D-mannose sugar, gas-liquid chromatography of the whole cell hydrolysates indicated that a spectrum of eight sugars (rhamnose, xylose, galactose, 2-O-methyl-D-mannose, glucose, and inositol) is a better Frankia marker.

v Frankia can now be cultured in industrial fermenters, broken down in blenders, and applied on a large scale by conventional greenhouse watering systems with the filters removed. It requires about one 15 ml tube (one colony) of Frankia isolate

to inoculate 50 alder seedlings. The operational methods are available and ready to use. A private sector laboratory (Les Laboratoires Rhizotec, Inc.) is already producing Frankia inocula on a commercial basis and there are export possibilities.

11.9 Survival of Frankia symbionts in the field

i Although selected rhizobial inocula on legumes tend to persist for only one to three years, the Frankia in perennial actinorhizal nodules may well persist for longer periods.

A range of alder and Elaeagnus species was inoculated with selected Frankia ($ACNI^{AG}$, $AGNI^{AG}$, $EUNI_f20$) and established in a forest soil for future observation, but the plants are still too young to yield results. It appears that some of the Elaeagnus inocula are sensitive to transport and that it is better to inoculate plants near the Frankia bank. Recent observations that some strains of Frankia are highly specific in their responses to antibiotics will greatly facilitate studies of the persistence of selected Frankia strains in the field.

11.10 Relationships between actinorhizal symbioses, mycorrhizae, and the rhizosphere

i Contrary to suggestions in the literature that alder is highly specific concerning its ectomycorrhizal symbionts, the ENFOR-supported research showed that many fungi (e.g. species of Alpova, Cenococcum, Cortinarius, Hebeloma, Laccaria, Leccinum, Paxillus, Pisolithus and Scleroderma) form ectomycorrhizae with Alnus rugosa.

ii The morphology of the ectomycorrhizae differed from the usual type occurring in the Pinaceae by forming Hartig nets that are mainly epidermal, penetrating only a little into the root cortex. (The common form is for the Hartig nets to be deeply embedded in the cortex.)

iii It was concluded that these cortical and epidermal Hartig nets could be used to differentiate between ectomycorrhizae of the Betulaceae (e.g. birch and alder) type. Alpova diplophloeus formed well developed ectomycorrhizae on Alnus, but even this fungus only formed a superficial, epidermal Hartig net.

iv Since nodulated roots of alder accept ectomycorrhizal inoculants, nodulation does not appear to modify the mycorrhiza recognition system. This raises many questions about infectivity mechanisms.

v Several fungi that form ectomycorrhizae with alder also form ectomycorrhizae with other trees such as pines. Theoretically the network of hyphae of these common ectomycorrhizae in forest soils could provide pathways for nitrogen fixed by the alder to trees that are unable to fix nitrogen.

vi $^{15}N_2$ was used as an isotope tracer to test the hypothesis that mycorrhizal hyphae act as pathways for fixed nitrogen. ^{15}N appeared in the non-fixing pine but the quantities were too small to be conclusive. Further research is required into this hypothesis using more sensitive techniques.

vii The literature suggests that more nitrogen is fixed in the rhizosphere of forest plants than is usually accepted. However, an experiment measuring nitrogen fixed in rhizospheres of unnodulated alder and poplar indicated that, although nitrogen was fixed in very small quantities in the rhizospheres, it was not sufficient to draw firm conclusions. Nitrogen fixation in tree rhizospheres needs further study.

viii The ectomycorrhizal fungi collected during this work represents a useful bank of genetic material for future work.

11.11 General conclusions

i The ENFOR program at Laval University has provided a basis for future research and development, and the Frankia inoculation technique is already in operational use.

ii The program has filled a large gap in Canada's forest science, producing graduates at the masters and doctoral level trained in nitrogen fixation and mycorrhizal symbioses of forest plants. Earlier there were only a few in Canada. The ENFOR funds provided seed-money that attracted other funding, and have resulted in the production of many theses and publications (see 'Literature'). It is concluded that the Laval University work has fulfilled the objective of providing a scientific and technological basis for future operations involving plants with nitrogen-fixing symbioses.

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APPENDIX I

BIOMASS AND NUTRIENT REGRESSION EQUATIONS

Code

PH = *Populus* hybrid
PT = *P. tremuloides*
PB = *P. balsamifera*
S = *Salix* spp.
PG = *Pinus banksiana*
AG = *Alnus glutinosa*
AR = *A. rugosa*
AC = *A. crispa*

Table (i): Biomass (g)
$\log \hat{Y}$: a + b log $(D^2H)^1$

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	92.18	18.7435	-2.04598	0.79674
PT	84.29	1.6332	-2.45038	0.81570
PB	78.36	5.6913	-2.11550	0.80719
S	71.38	8.3389	-2.02672	0.75518
PG	91.14	6.3767	-1.60083	0.74552
AG	96.05	8.035	-2.10940	0.80872
AR	70.80	9.341	-2.05398	0.78894
AC	78.05	6.935	-2.19191	0.85758
2: Stem + Branches				
PH	94.05	41.0976	-1.82382	0.83384
PT	95.30	2.3483	-2.54173,	0.96041
PB	84.27	7.6397	-1.61057	0.74620
S	75.81	25.7974	-1.85492	0.83494
PG	96.45	3.5342	-2.17477	0.87357
AG	97.48	13.314	-2.32656	0.91943
AR	80.21	14.226	-1.89140	0.82296
AC	85.75	9.597	-2.21050	0.92835
3: Total				
PH	94.02	57.260	-1.61999	0.82208
PT	94.88	3.320	-2.25793	0.92210
PB	84.89	11.702	-1.42278	0.74844
S	75.57	33.443	-1.64264	0.81331
PG	94.51	9.366	-1.54271	0.79963
AG	97.28	20.437	-1.96328	0.87979
AR	79.92	21.267	-1.61803	0.80085
AC	83.92	16.007	-1.90849	0.90065

D = diameter
H = height

Table (ii): Nitrogen Content ($g \times 10^{-2}$)
$\log \hat{Y}$: a + b log (D^2H)

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	85.55	22.9684	−1.84542	0.74089
PT	83.93	2.7920	−2.38162	0.85314
PB	80.41	9.0719	−2.39330	0.92487
S	65.67	14.1606	−1.86670	0.75401
PG	91.10	11.0411	−1.38033	0.74928
AG	94.45	25.421	−1.62124	0.79359
AR	68.73	24.390	−1.71083	0.79865
AC	78.63	16.431	−1.94774	0.88945
2: Stem + Branches				
PH	89.59	30.5115	−1.75638	0.76628
PT	94.34	2.8152	−2.61771	0.97549
PB	84.47	7.4384	−1.71566	0.76824
S	65.57	17.8270	−1.69945	0.73993
PG	94.05	3.3819	−2.29084	0.86488
AG	95.62	19.291	−2.00014	0.85570
AR	78.23	20.615	−1.57676	0.78347
AC	95.74	13.112	−2.08162	0.92934
3: Total				
PH	89.38	50.0809	−1.49228	0.75598
PT	93.05	4.6113	−2.23605	0.93138
PB	84.14	14.2427	−1.66125	0.82520
S	67.07	31.0162	−1.46458	0.74506
PG	92.32	14.0517	−1.35547	0.77664
AG	95.65	41.199	−1.47588	0.81913
AR	77.95	39.098	−1.28066	0.77869
AC	83.29	28.406	−1.70394	0.90766

Table (iii): Phosphorus content ($g \times 10^{-6}$)
$\log \hat{Y}$: a + b log (D^2H)

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	86.90	27.704	0.71708	1.17497
PT	80.94	3.400	0.30472	1.26334
PB	81.70	8.280	0.07402	1.41793
S	52.09	17.120	1.18473	0.99107
PG	89.60	11.815	1.31080	1.14000
AG	85.05	26.037	0.82663	0.19063
AR	70.61	14.644	0.64375	1.23945
AC	76.56	9.925	0.53452	1.29766
2: Stem + Branches				
PH	88.78	37.572	1.09154	1.12399
PT	93.37	3.056	−0.10282,	1.48677
PB	88.72	7.261	0.70260	1.25152
S	69.36	20.821	0.94670	1.14126
PG	93.82	4.610	0.67865	1.25657
AG	95.13	16.159	0.65209	1.27106
AR	79.47	17.434	1.04215	1.18299
AC	86.08	9.520	0.64835	1.31167
3: Total				
PH	89.56	60.137	1.25032	1.14152
PT	92.56	5.264	0.33640	1.40898
PB	87.76	13.827	0.82053	1.29448
S	64.10	36.538	1.37669	1.06991
PG	92.01	15.455	1.38722	1.17612
AG	91.87	39.738	1.04004	1.23304
AR	80.92	27.070	1.23505	1.18955
AC	83.83	18.155	0.91647	1.30061

Table (iv): Magnesium content ($g \times 10^{-6}$)
$\log \hat{Y}$: a + b log (D^2H)

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	77.26	116.929	1.48122	1.08971
PT	74.25	4.707	0.78859	1.11942
PB	74.22	16.333	1.76478	0.94415
S	71.72	36.502	0.87064	1.24132
PG	88.03	8.608	1.18688	1.12291
AG	87.14	47.117	0.29320	1.42374
AR	59.03	22.761	0.42304	1.31607
AC	67.71	20.061	0.83125	1.25678
2: Stem + Branches				
PH	85.71	70.875	1.45084	1.08276
PT	94.42	2.498	−0.02129	1.44630
PB	81.02	9.282	1.20632	1.07093
S	73.42	29.533	0.73566	1.26059
PG	94.91	4.547	0.49332	1.33041
AG	95.19	16.209	0.17205	1.40761
AR	79.87	10.225	0.73999	1.20560
AC	83.61	11.722	0.53078	1.31683
3: Total				
PH	82.59	179.049	1.78463	1.08381
PT	91.01	5.864	0.62200	1.31311
PB	79.24	23.593	1.89022	0.97748
S	74.25	61.898	1.19175	1.22564
PG	92.39	12.284	1.21454	1.20347
AG	91.21	60.538	0.53491	1.41926
AR	73.48	27.151	1.04339	1.21249
AC	76.37	31.671	1.02579	1.27572

Table (v): Calcium content ($g \times 10^{-6}$)
$\log \hat{Y}$: a + b log (D^2H)

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	83.05	248.073	2.20763	0.72746
PT	82.69	21.271	1.88783	0.75515
PB	72.58	40.228	2.67665	0.57527
S	65.00	138.213	2.24871	0.72641
PG	84.98	17.779	2.27918	0.61505
AG	93.58	108.901	1.34864	0.91803
AR	67.80	79.182	1.48054	0.86372
AC	78.30	62.496	1.73718	0.86406
2: Stem + Branches				
PH	90.99	148.067	2.24686	0.71441
PT	91.57	22.391	1.02149	1.02358
PB	55.45	81.451	2.80001	0.56848
S	67.14	163.816	2.23850	0.74932
PG	93.25	5.576	1.03773	0.83145
AG	92.05	118.667	1.34216	0.91477
AR	74.64	85.727	1.63463	0.85861
AC	81.51	63.611	1.39394	0.95844
3: Total				
PH	88.12	373.165	2.53647	0.72028
PT	91.92	36.200	1.69439	0.91250
PB	63.25	115.483	3.15021	0.54664
S	67.50	290.122	2.59001	0.72907
PG	88.84	22.500	2.20929	0.67221
AG	93.45	216.266	1.64977	0.91627
AR	78.43	132.333	1.96710	0.84027
AC	82.46	115.127	1.89561	0.90581

Table (vi): Potassium content ($g \times 10^{-6}$)
$\log \hat{Y}$: a + b log (DH)

Species	R^2(%)	Sy	a	b
1: Leaf				
PH	84.66	223.164	0.76751	1.38705
PT	77.99	11.474	0.86154	1.23769
PB	79.62	35.085	0.42474	1.49263
S	62.50	109.732	1.27001	1.22819
PG	88.41	29.721	1.36144	1.24007
AG	89.03	46.283	1.21700	1.17837
AR	62.98	62.617	0.59003	1.41130
AC	80.33	23.338	0.75524	1.36523
2: Stem + Branches				
PH	89.82	169.921	1.74699	1.13156
PT	95.90	6.591	0.66890	1.38382
PB	90.04	18.643	1.35992	1.18533
S	72.87	96.176	1.08508	1.30513
PG	93.66	16.657	1.03377	1.31912
AG	95.75	28.754	0.83521	1.29984
AR	82.22	31.561	1.19801	1.22692
AC	86.15	19.679	0.87511	1.34045
3: Total				
PH	89.50	350.049	1.66650	1.23289
PT	94.33	12.947	1.05028	1.32700
PB	90.08	39.773	1.34440	1.29369
S	70.54	193.064	1.48991	1.26621
PG	91.66	43.803	1.53262	1.26962
AG	94.59	62.606	1.38940	1.22159
AR	80.30	70.725	1.31684	1.28566
AC	85.68	38.990	1.14033	1.34714

APPENDIX II

TREE BIOMASS AT ST. LAMBERT, VILLEROY, ST. LOUIS, AND AMOS

Tree Codes

PH	=	*Populus* hybrid
PT	=	*P. tremuloides*
PB	=	*P. balsamifera*
S	=	*Salix* spp.
PG	=	*Pinus banksiana*
AR	=	*Alnus rugosa*
AC	=	*A. crispa*
AG	=	*A. glutinosa*

Table (i): Stem biomass in g per tree with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	231 (38.8)	174 (27.2)	422 (32.0)	102 (17.1)
PT	12 (2.6)	14 (3.0)	4 (0.7)	
PB	15 (2.0)	33 (4.6)		
S	72 (10.1)	25 (4.5)	79 (8.3)	54 (6.4)
PG			50 (4.4)	7 (0.6)
PH-AR	90 (16.8)	187 (59.6)	236 (32.8)	
PH-AC	227 (71.8)	232 (89.6)	290 (59.7)	81 (10.5)
PT-AR	31 (6.9)	25 (4.4)	26 (9.3)	
PT-AC	14 (3.7)	32 (8.3)	24 (8.2)	
PB-AG	107 (40.4)	65 (10.2)		
S-AR	86 (15.2)	30 (4.0)	52 (6.1)	
S-AC	110 (45.9)	38 (5.9)	69 (10.7)	52 (6.1)
PG-AR			41 (3.5)	
PG-AC			61 (6.2)	17 (1.8)
AG	540 (210)	62 (12.1)		
AR	31 (3.2)	42 (4.9)	37 (2.3)	
AC	24 (5.5)	38 (7.7)	57 (9.7)	28 (2.3)

Table (ii): Leaf biomass in g per tree with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	87 (13.5)	67 (9.6)	158 (11.3)	40 (6.0)
PT	4 (0.6)	4 (0.7)	1.5 (0.19)	
PB	8 (1.3)	20 (3.2)		
S	21 (2.4)	8 (1.2)	23 (2.0)	16 (1.6)
PG			48 (3.4)	9 (0.6)
PH-AR	36 (5.9)	70 (18.5)	90 (10.5)	
PH-AC	31 (19.1)	81 (22.1)	105 (16.3)	33 (3.4)
PT-AR	13 (2.8)	10 (1.6)	12 (3.8)	
PT-AC	6 (1.3)	14 (3.2)	12 (3.8)	
PB-AG	48 (15.5)	37 (6.0)		
S-AR	27 (3.9)	12 (1.5)	19 (1.9)	
S-AC	30 (8.0)	17 (2.5)	23 (2.7)	17 (1.5)
PG-AR			32 (2.6)	
PG-AC			45 (4.4)	12 (0.8)
AG	190 (51)	30 (4.5)		
AR	15 (1.5)	20 (2.2)	18 (1.1)	
AC	13 (2.5)	19 (3.3)	28 (4.0)	15 (1.1)

Table (iii): Aboveground biomass in g per tree with standard error of mean in brackets. Fall 1981

	St Lambert	Villeroy	St Louis	Amos
PH	319 (52.2)	241 (36.8)	582 (43.3)	142 (23.0)
PT	17 (3.2)	19 (3.6)	6 (0.9)	
PB	24 (3.2)	52 (7.4)		
S	93 (12.5)	33 (5.7)	102 (10.3)	70 (7.9)
PG			97 (7.5)	16 (1.3)
PH-AR	126 (22.2)	255 (75.3)	325 (42.5)	
PH-AC	306 (87.1)	310 (105.9)	393 (73.6)	114 (13.5)
PT-AR	45 (9.7)	37 (6.1)	38 (13.3)	
PT-AC	20 (5.0)	46 (11.4)	37 (12.0)	
PB-AG	154 (53.4)	101 (15.4)		
S-AR	113 (18.5)	43 (5.5)	71 (8.0)	
S-AC	137 (49.2)	55 (8.3)	92 (13.0)	69 (7.4)
PG-AR			73 (5.7)	
PG-AC			105 (10.3)	28 (2.4)
AG	720 (242)	92 (16.4)		
AR	47 (4.6)	63 (7.0)	56 (3.4)	
AC	36 (7.9)	57 (10.9)	85 (13.5)	43 (3.4)

Table (iv): Stem biomass in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St Lambert	Villeroy	St Louis	Amos
PH	3210 (539)	2410 (378)	5870 (445)	1410 (237)
PT	170 (37)	200 (41)	56 (10 0)	
PB	210 (28)	460 (65)		
S	1010 (140)	350 (63)	1100 (116)	750 (89)
PG			690 (61)	95 (8 8)
PH AR	1240 (234)	2590 (827)	3280 (456)	
PH AC	3160 (997)	3200 (1240)	4030 (829)	1130 (145)
PT AR	430 (95)	350 (61)	360 (129)	
PT AC	190 (52)	440 (115)	340 (114)	
PB AG	1490 (562)	900 (142)		
S AR	1190 (212)	420 (55)	720 (85)	
S AC	1530 (638)	530 (82)	950 (149)	720 (85)
PG AR			570 (49)	
PG AC			840 (87)	230 (25)
AG	7560 (2916)	860 (168)		
AR	430 (44)	590 (69)	520 (33)	
AC	330 (77)	530 (107)	800 (134)	400 (32)

Table (v): Leaf biomass in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	1210 (188)	930 (134)	2200 (156)	550 (84)
PT	50 (8)	60 (9)	21 (2.7)	
PB	120 (18)	270 (44)		
S	280 (34)	110 (17)	310 (28)	220 (22)
PG			660 (47)	121 (8.8)
PH-AR	500 (81)	980 (257)	1250 (146)	
PH-AC	1130 (265)	1100 (310)	1460 (227)	450 (47)
PT-AR	180 (39)	150 (23)	160 (53)	
PT-AC	80 (18)	190 (45)	170 (53)	
PB-AG	670 (215)	520 (83)		
S-AR	380 (54)	170 (21)	260 (27)	
S-AC	410 (111)	230 (34)	320 (38)	240 (21)
PG-AR			440 (36)	
PG-AC			620 (61)	160 (11)
AG	2620 (707)	410 (63)		
AR	210 (21)	280 (31)	250 (15)	
AC	170 (34)	270 (46)	390 (56)	210 (15)

Table (vi): Total aboveground biomass in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	4430 (725)	3350 (512)	8080 (601)	1970 (320)
PT	230 (45)	260 (50)	78 (12.7)	
PB	330 (44)	720 (102)		
S	1300 (174)	460 (80)	1420 (143)	970 (110)
PG			1340 (105)	217 (17.6)
PH-AR	1750 (309)	3550 (1046)	4520 (591)	
PH-AC	4250 (1210)	4300 (1470)	5460 (1022)	1580 (188)
PT-AR	620 (135)	510 (85)	530 (185)	
PT-AC	270 (70)	640 (159)	510 (167)	
PB-AG	2140 (741)	1400 (214)		
S-AR	1570 (258)	600 (76)	990 (111)	
S-AC	1910 (684)	760 (115)	1270 (180)	960 (102)
PG-AR			1010 (80)	
PG-AC			1460 (143)	390 (33)
AG	9930 (3360)	1270 (227)		
AR	650 (64)	880 (98)	780 (47)	
AC	510 (110)	790 (151)	1180 (188)	600 (47)

Table (vii): Total aboveground biomass of hybrid poplars in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	319 (52.2) BC[1]	241 (36.8) BC	582 (43.3) A	142 (23.0) E
PH-AR	221 (50.0) CD	479 (149.1) AB	490 (53.3) A	
PH-AC	437 (69.4) AB	395 (49.3) AB	563 (50.0) A	188 (27.7) DE

[1] BMDP 3V pair-wise t-test. When letters are the same, there is no significant difference at P = 0.05.

Table (viii): Total aboveground biomass of *Populus tremuloides* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
PT	17 (3.2) AB	19 (3.6) AB	6 (0.9) C
PT-AR	23 (7.2) AB	29 (9.6) A	5 (1.1) C
PT-AC	14 (4.3) B	21 (5.9) AB	5 (1.2) C

Table (ix): Total aboveground biomass of *Populus balsamifera* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy
PB	24 (3.2) B	52 (7.4) A
PB-AG	19 (2.4) B	110 (30.0) A

Table (x): Total aboveground biomass of *Salix alba* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
S	93 (12.5) AB	33 (5.7) C	102 (10.3) A	70 (7.9) ABC
S-AR	178 (47.0) A	43 (10.7) BC	96 (20.1) A	
S-AC	140 (31.0) A	39.3 (8.2) BC	101 (12.7) A	119 (21.2) A

Table (xi): Total aboveground biomass of *Pinus banksiana* in g per tree with standard error of mean in brackets, Fall 1982

	St Louis	Amos
PG	97 (7.5) A	16 (1.3) B
PG-AR	92 (11.9) A	
PG-AC	91 (6.7) A	15 (1.2) B

Table (xii): Total aboveground biomass of *Alnus glutinosa* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy
AG	720 (242) A	92 (16.4) B
AG-PB	380 (182) A	91 (14.6) B

Table (xiii): Total aboveground biomass of *Alnus rugosa* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
AR	47 (4.6) B	63 (7.0) B	56 (3.4) B
AR-PH	45 (6.7) B	56 (11.8) B	77 (6.8) A
AR-PT	57 (11.4) B	37 (4.2) B	53 (6.0) B
AR-S	59 (9.2) B	42 (5.3) B	53 (5.8) B
AR-PG			53 (4.2) B

Table (xiv): Total aboveground biomass of *Alnus crispa* in g per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
AC	36 (7.9) CD	57 (10.9) BC	85 (13.5) AB
AC-PH	54 (11.4) BC	45 (10.6) CD	83 (12.1) AB
AC-PT	28 (10.6) D	73 (23.7) ABC	60 (16.4) BC
AC-S	67 (45.8) ABC	67 (13.7) ABC	71 (17.4) ABC
AC-PG			121 (25.5) A

APPENDIX III

TREE NUTRIENT CONTENT ON THE PLOTS AT ST-LAMBERT, VILLEROY, AND AMOS

Tree Codes

PH = *Populus* hybrid
PT = *P. tremuloides*
PB = *P. balsamifera*
S = *Salix* spp.
PG = *Pinus banksiana*
AG = *Alnus glutinosa*
AR = *A. rugosa*
AC = *A. crispa*

Table (i): Stem nitrogen content in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	117 (16.9)	90 (12.2)	210 (14.2)	54 (7.6)
PT	12 (2.6)	14 (3.0)	4 (0.7)	
PB	15 (2.0)	33 (4.8)		
S	37 (4.3)	14 (2.1)	41 (3.6)	28 (2.7)
PG			35 (3.0)	5 (0.4)
PH-AR	61 (7.7)	106 (20.1)	132 (10.6)	
PH-AC	117 (21.3)	115 (24.2)	155 (18.1)	55 (5.1)
PT-AR	42 (10.7)	34 (6.8)	40 (20.0)	
PT-AC	17 (4.9)	41 (12.1)	35 (14.9)	
PB-AG	110 (40)	69 (10.9)		
S-AR	60 (8.0)	32 (4.4)	44 (4.7)	
S-AC	62 (17.1)	41 (7.0)	51 (6.4)	36 (3.2)
PG-AR			42 (4.0)	
PG-AC			62 (6.9)	21 (2.9)
AG	470 (147)	64 (10.9)		
AR	43 (4.2)	58 (6.3)	52 (3.1)	
AC	32 (7.5)	52 (10.5)	78 (13.2)	39 (3.2)

Table (ii): Leaf nitrogen content in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St-Louis	Amos
PH	70 (9.5)	55 (7.0)	124 (8.0)	33 (4.4)
PT	7 (1.1)	7 (1.2)	2 (0.3)	
PB	13 (2.6)	36 (7.7)		
S	29 (3.5)	11 (1.7)	32 (2.9)	22 (2.2)
PG			82 (5.9)	15 (1.1)
PH-AR	42 (5.1)	70 (12.1)	87 (6.1)	
PH-AC	74 (10.6)	70 (11.2)	100 (9.2)	39 (3.2)
PT-AR	32 (8.6)	25 (4.9)	32 (15.5)	
PT-AC	13 (3.5)	32 (9.7)	32 (13.9)	
PB-AG	140 (70)	94 (19.9)		
S-AR	50 (6.9)	26 (3.9)	37 (4.1)	
S-AC	49 (12.3)	37 (6.7)	43 (5.1)	31 (2.7)
PG-AR			60 (4.6)	
PG-AC			89 (8.5)	24 (1.8)
AG	470 (121)	78 (11.4)		
AR	37 (3.7)	50 (5.5)	44 (2.7)	
AC	30 (6.3)	46 (8.7)	69 (10.7)	36 (2.7)

Table (iii): Total aboveground nitrogen content in g × 10^{-2} per tree with standard error of mean in brackets. Fall 1981

	St-Lambert	Villeroy	St Louis	Amos
PH	189 (26.7)	147 (19.4)	338 (22.4)	88 (12.1)
PT	19 (3.8)	22 (4.3)	6 (1.1)	
PB	28 (4.4)	67 (11.3)		
S	67 (7.8)	26 (3.9)	74 (6.5)	51 (5.0)
PG			117 (8.7)	20 (1.5)
PH-AR	105 (12.8)	177 (31.9)	222 (16.6)	
PH-AC	193 (31.4)	186 (34.5)	256 (26.9)	95 (8.3)
PT-AR	75 (19.6)	61 (12.0)	75 (37.0)	
PT-AC	30 (8.5)	74 (21.8)	67 (28.8)	
PB-AG	240 (100)	158 (27.6)		
S-AR	111 (14.9)	59 (8.4)	83 (8.9)	
S-AC	111 (29.2)	78 (13.6)	94 (11.5)	68 (6.0)
PG-AR			102 (7.6)	
PG-AC			151 (14.5)	44 (4.0)
AG	940 (262)	144 (22.4)		
AR	81 (7.8)	109 (11.7)	98 (5.7)	
AC	63 (13.9)	98 (19.1)	147 (23.7)	75 (5.9)

Table (iv): Stem nitrogen content in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St Louis	Amos
PH	16.3 (2.35)	12.6 (1.69)	29.1 (1.97)	7.5 (1.06)
PT	1.7 (0.37)	1.9 (0.42)	0.53 (0.098)	
PB	2.0 (0.28)	4.5 (0.67)		
S	5.1 (0.59)	2.0 (0.30)	5.6 (0.50)	3.9 (0.38)
PG			4.8 (0.42)	0.67 (0.062)
PH-AR	8.4 (1.07)	14.7 (2.80)	18.4 (1.47)	
PH-AC	16.3 (2.96)	15.9 (3.36)	21.5 (2.51)	7.6 (0.71)
PT-AR	5.8 (1.48)	4.7 (0.94)	5.6 (2.77)	
PT-AC	2.3 (0.68)	5.6 (1.68)	4.8 (2.06)	
PB-AG	15 (5.5)	9.5 (1.51)		
S-AR	8.3 (1.11)	4.4 (0.61)	6.1 (0.65)	
S-AC	8.6 (2.38)	5.7 (0.98)	7.1 (0.89)	5.1 (0.45)
PG-AR			5.8 (0.55)	
PG-AC			8.6 (0.96)	2.9 (0.41)
AG	65 (20.4)	8.9 (1.51)		
AR	6.0 (0.58)	8.1 (0.87)	7.2 (0.43)	
AC	4.5 (1.05)	7.2 (1.46)	10.8 (1.83)	5.4 (0.44)

Table (v): Leaf nitrogen content in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St-Lambert	Villeroy	St Louis	Amos
PH	9.7 (1.32)	7.6 (0.97)	17.2 (1.11)	4.6 (0.60)
PT	0.9 (0.15)	1.0 (0.17)	0.33 (0.046)	
PB	1.9 (0.36)	5.0 (1.06)		
S	4.1 (0.48)	1.6 (0.24)	4.5 (0.40)	3.1 (0.31)
PG			11.5 (0.82)	2.07 (0.15)
PH-AR	5.9 (0.70)	9.7 (1.68)	12.0 (0.84)	
PH-AC	10.3 (1.47)	9.8 (1.56)	13.8 (1.28)	5.4 (0.45)
PT-AR	4.5 (1.20)	3.4 (0.68)	4.4 (2.16)	
PT-AC	1.8 (0.48)	4.5 (1.35)	4.4 (1.93)	
PB-AG	19 (9.7)	13.1 (2.76)		
S-AR	6.9 (0.95)	3.7 (0.55)	5.1 (0.57)	
S-AC	6.8 (1.71)	5.1 (0.93)	5.9 (0.71)	4.4 (0.38)
PG-AR			8.4 (0.64)	
PG-AC			12.3 (1.18)	3.3 (0.26)
AG	65 (16.8)	10.8 (1.58)		
AR	5.1 (0.51)	6.9 (0.77)	6.2 (0.37)	
AC	4.1 (0.88)	6.5 (1.20)	9.6 (1.48)	4.9 (0.38)

Table (vi): Total aboveground nitrogen content in kg ha^{-1} with standard error of mean in brackets, Fall 1981

	St Lambert	Villeroy	St Louis	Amos
PH	26.3 (3.71)	20.4 (2.69)	46.9 (3.11)	12.3 (1.68)
PT	2.6 (0.53)	3.0 (0.59)	0.88 (0.148)	
PB	3.9 (0.62)	9.3 (1.57)		
S	9.3 (1.09)	3.6 (0.54)	10.2 (0.91)	7.1 (0.70)
PG			16.2 (1.21)	2.75 (0.214)
PH AR	14.6 (1.78)	24.6 (4.43)	30.8 (2.30)	
PH AC	26.8 (4.36)	25.8 (4.79)	35.6 (3.73)	13.1 (1.15)
PT AR	10.5 (2.72)	8.4 (1.67)	10.4 (5.14)	
PT AC	4.1 (1.17)	10.3 (3.03)	9.3 (4.00)	
PB AG	34 (13.9)	21.9 (3.84)		
S AR	15.3 (2.06)	8.2 (1.17)	11.5 (1.23)	
S AC	15.4 (4.06)	10.8 (1.89)	13.1 (1.60)	9.5 (0.83)
PG AR			14.2 (1.05)	
PG AC			20.9 (2.02)	6.1 (0.55)
AG	130 (36.4)	19.9 (3.11)		
AR	11.3 (1.08)	15.2 (1.62)	13.6 (0.80)	
AC	8.7 (1.92)	13.6 (2.65)	20.4 (3.29)	10.4 (0.82)

Table (vii) Stem phosphorus content in g × 10^{-3} per tree with standard error of mean in brackets. Fall 1982

	St Lambert	Villeroy	St Louis	Amos
PH	136(17.8)	109(14.2)	252(18.4)	61(8.2)
PT	14(3.3)	17(4.2)	4(0.45)	
PB	17(2.7)	41(7.3)		
S	45(6.3)	18(2.9)	55(4.3)	13(1.4)
PG			22(3.0)	7.2(0.64)
PH AB	65(8.8)	120(25.9)	150(13.3)	
PH AC	132(28.1)	138(36.3)	173(23.4)	64(5.1)
PT AB	38(8.9)	81(6.0)	39(7.9)	
PT AC	14(3.8)	35(8.9)	27(9.3)	
PB AC	82(25.9)	71(12.4)		
S AB	62(8.3)	51(4.0)	48(3.3)	
S AC	66(19.8)	36(5.3)	53(6.7)	30(3.4)
PG AB			44(3.1)	
PG AC			58(8.3)	17(1.9)
AC	390(100)	53(8.7)		
AB	37(3.5)	49(5.2)	46(2.3)	
AC	25(5.5)	40(8.3)	55(8.2)	28(2.2)

Table (viii): Leaf phosphorus content in g × 10^{-3} per tree with standard error of mean in brackets. Fall 1982

	St Lambert	Villeroy	St Louis	Amos
PH	90 (12 7)	72 (10 0)	169 (11 6)	39 (5 8)
PT	7 (1 2)	8 (1 5)	2 8 (0 41)	
PB	13 (2 6)	35 (8 3)		
S	24 (2 3)	11 (1 4)	29 (2 1)	18 (1 5)
PG			79 (5 6)	15 1 (1 15)
PH AR	41 (5 7)	80 (19 2)	99 (9 5)	
PH AC	86 (17 6)	89 (22 2)	114 (15 3)	35 (3 4)
PT AR	20 (4 2)	16 (2 5)	19 (6 4)	
PT AC	9 (1 9)	20 (4 5)	17 (4 8)	
PB AG	66 (23 3)	65 (13 5)		
S AR	33 (4 0)	18 (2 0)	26 (2 5)	
S AC	36 (9 1)	23 (3 4)	31 (3 5)	21 (1 7)
PG AR			52 (4 5)	
PG AC			71 (7 6)	17 (1 2)
AG	240 (58)	42 (6 1)		
AR	22 (2 2)	30 (3 4)	28 (1 7)	
AC	17 (3 7)	28 (5 6)	38 (5 6)	19 (1 5)

Table (ix): Total aboveground phosphorus content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	228 (30.7)	183 (24.5)	426 (28.2)	102 (14.1)
PT	22 (4.3)	26 (5.8)	7.6 (1.40)	
PB	29 (5.2)	75 (14.4)		
S	69 (7.4)	29 (4.2)	85 (6.9)	52 (4.7)
PG			124 (9.2)	22.4 (1.80)
PH-AR	108 (14.1)	202 (44.1)	252 (22.8)	
PH-AC	220 (46.0)	230 (58.7)	290 (39.4)	91 (8.8)
PT-AR	60 (13.2)	48 (8.6)	60 (25.0)	
PT-AC	24 (5.8)	54 (13.5)	44 (14.1)	
PB-AG	148 (47.3)	133 (24.1)		
S-AR	95 (12.0)	49.3 (6.0)	75 (7.4)	
S-AC	102 (28.1)	60 (8.8)	85 (10.1)	58 (5.0)
PG-AR			96 (7.3)	
PG-AC			129 (12.3)	34 (2.6)
AG	590 (156)	96 (14.8)		
AR	60 (5.8)	81 (8.5)	76 (4.5)	
AC	42 (9.3)	69 (13.8)	94 (13.8)	48 (3.7)

Table (x): Stem phosphorus content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	1.88 (0.248)	1.52 (0.198)	3.50 (0.227)	0.85 (0.114)
PT	0.19 (0.042)	0.23 (0.058)	0.063 (0.0132)	
PB	0.23 (0.038)	0.57 (0.102)		
S	0.63 (0.074)	0.25 (0.040)	0.77 (0.068)	0.46 (0.046)
PG			0.62 (0.050)	0.100 (0.0089)
PH-AR	0.90 (0.116)	1.67 (0.356)	2.09 (0.185)	
PH-AC	1.84 (0.391)	1.93 (0.504)	2.40 (0.331)	0.76 (0.074)
PT-AR	0.52 (0.123)	0.43 (0.083)	0.55 (0.264)	
PT-AC	0.20 (0.053)	0.46 (0.123)	0.37 (0.129)	
PB-AG	1.14 (0.359)	0.99 (0.172)		
S-AR	0.86 (0.116)	0.43 (0.056)	0.66 (0.069)	
S-AC	0.92 (0.276)	0.50 (0.076)	0.74 (0.093)	0.50 (0.048)
PG-AR			0.62 (0.051)	
PG-AC			0.80 (0.076)	0.23 (0.023)
AG	4.9 (1.39)	0.73 (0.121)		
AR	0.51 (0.049)	0.68 (0.072)	0.65 (0.038)	
AC	1.34 (0.076)	0.56 (0.115)	0.77 (0.114)	0.39 (0.030)

Table (xi): Leaf phosphorus content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St Lambert	Villeroy	St-Louis	Amos
PH	1.24 (0.176)	0.99 (0.139)	2.35 (0.162)	0.55 (0.080)
PT	0.10 (0.016)	0.12 (0.021)	0.039 (0.0057)	
PB	0.17 (0.037)	0.49 (0.115)		
S	0.33 (0.032)	0.15 (0.019)	0.40 (0.030)	0.26 (0.020)
PG			1.10 (0.078)	0.209 (0.0160)
PH-AR	0.57 (0.080)	1.12 (0.266)	1.37 (0.132)	
PH-AC	1.19 (0.245)	1.24 (0.309)	1.59 (0.212)	0.49 (0.047)
PT-AR	0.28 (0.058)	0.22 (0.035)	0.27 (0.090)	
PT-AC	0.12 (0.027)	0.28 (0.063)	0.23 (0.067)	
PB-AG	0.92 (0.323)	0.90 (0.188)		
S-AR	0.46 (0.055)	0.25 (0.028)	0.37 (0.035)	
S-AC	0.50 (0.126)	0.33 (0.047)	0.43 (0.049)	0.29 (0.023)
PG-AR			0.72 (0.063)	
PG-AC			0.99 (0.105)	0.24 (0.017)
AG	3.35 (0.809)	0.58 (0.085)		
AR	0.31 (0.031)	0.42 (0.047)	0.39 (0.024)	
AC	0.24 (0.052)	0.39 (0.078)	0.53 (0.077)	0.27 (0.021)

Table (xii): Total aboveground phosphorus content in kg ha $^{-1}$ with standard error of mean in brackets, Fall 1982

	St Lambert	Villeroy	St Louis	Amos
PH	3.17 (0.427)	2.54 (0.340)	5.91 (0.392)	1.42 (0.196)
PT	0.30 (0.060)	0.36 (0.080)	0.105 (0.0194)	
PB	0.41 (.072)	1.04 (0.200)		
S	0.96 (0.103)	0.40 (0.058)	1.17 (0.095)	0.72 (0.065)
PG			1.72 (0.128)	0.311 (0.0249)
PH-AR	1.49 (0.195)	2.81 (0.613)	3.50 (0.317)	
PH-AC	3.06 (0.639)	3.20 (0.816)	4.03 (0.547)	1.26 (0.122)
PT-AR	0.83 (0.183)	0.67 (0.119)	0.83 (0.347)	
PT-AC	0.33 (0.081)	0.75 (0.188)	0.61 (0.196)	
PB-AG	2.05 (0.657)	1.85 (0.334)		
S-AR	1.32 (0.167)	0.69 (0.083)	1.04 (0.102)	
S-AC	1.42 (0.390)	0.83 (0.123)	1.18 (0.141)	0.80 (0.069)
PG-AR			1.34 (0.101)	
PG-AC			1.79 (0.171)	0.47 (0.036)
AG	8.3 (2.17)	1.33 (0.206)		
AR	0.84 (0.081)	1.12 (0.118)	1.06 (0.063)	
AC	0.59 (0.129)	0.95 (0.192)	1.30 (0.191)	0.66 (0.051)

Table (xiii): Stem magnesium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	216 (26.8)	176 (21.5)	396 (24.5)	100 (12.5)
PT	12 (2.6)	15 (3.5)	4.2 (0.83)	
PB	15 (2.0)	32 (4.4)		
S	71 (9.8)	26 (4.9)	89 (9.1)	52 (6.1)
PG			51 (4.5)	7.5 (0.73)
PH-AR	93 (19.1)	190 (68.0)	235 (36.6)	
PH-AC	226 (74.6)	251 (107.9)	281 (60.1)	82 (10.7)
PT-AR	24 (4.7)	20 (3.3)	21 (6.7)	
PT-AC	12 (3.0)	27 (6.7)	20 (6.2)	
PB-AG	83 (26.7)	57 (8.5)		
S-AR	76 (14.5)	26 (3.4)	49 (6.3)	
S-AC	103 (43.7)	35 (5.3)	70 (11.3)	48 (5.9)
PG-AR			38 (3.3)	
PG-AC			55 (5.4)	14 (1.4)
AG	450 (171)	52 (10.5)		
AR	22 (2.1)	29 (3.1)	27 (1.6)	
AC	20 (4.4)	32 (6.6)	44 (6.6)	22 (1.7)

Table (xiv): Leaf magnesium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	246 (30.8)	200 (24.7)	453 (28.3)	114 (14.4)
PT	8 (1.1)	9 (1.3)	3.5 (0.41)	
PB	23 (2.5)	45 (5.0)		
S	84 (11.2)	30 (5.7)	104 (10.4)	61 (7.0)
PG			52 (3.7)	10.2 (0.76)
PH-AR	109 (25.2)	234 (97.3)	274 (45.5)	
PH-AC	244 (69.3)	265 (95.4)	309 (58.1)	91 (10.5)
PT-AR	21 (3.8)	16 (2.1)	18 (4.4)	
PT-AC	12 (2.3)	26 (5.7)	23 (6.4)	
PB-AG	123 (37.0)	77 (10.3)		
S-AR	90 (18.4)	29 (4.0)	57 (7.8)	
S-AC	114 (41.4)	43 (6.3)	81 (11.9)	57 (6.3)
PG-AR			40 (3.1)	
PG-AC			63 (5.5)	18 (1.4)
AG	700 (275)	79 (16.2)		
AR	23 (2.5)	32 (4.0)	29 (2.0)	
AC	25 (5.2)	40 (7.6)	55 (7.6)	29 (2.1)

Table (xv): Total aboveground magnesium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	471 (58.3)	382 (46.9)	863 (53.5)	218 (27.2)
PT	21 (3.7)	25 (4.8)	7.9 (1.26)	
PB	39 (4.4)	77 (9.1)	106 (13.4)	
S	155 (20.3)	57 (10.4)	191 (18.8)	113 (12.6)
PG			102 (7.8)	17.8 (1.48)
PH-AR	202 (42.5)	417 (152.8)	513 (81.5)	
PH-AC	475 (143.6)	520 (201.6)	597 (118.7)	176 (21.2)
PT-AR	46 (8.7)	38 (5.6)	40 (11.6)	
PT-AC	24 (5.5)	55 (12.6)	45 (13.1)	
PB-AG	208 (63.5)	133 (18.3)		
S-AR	164 (31.2)	56 (7.1)	106 (13.4)	
S-AC	215 (81.2)	79 (11.5)	151 (22.7)	104 (11.9)
PG-AR			77 (6.1)	
PG-AC			118 (10.7)	33 (2.8)
AG	1170 (454)	132 (27.1)		
AR	46 (4.5)	62 (6.7)	58 (3.5)	
AC	45 (9.6)	73 (14.2)	100 (14.1)	51 (3.8)

Table (xvi): Stem magnesium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	3.00 (0.372)	2.44 (0.299)	5.51 (0.341)	1.39 (0.174)
PT	0.17 (0.036)	0.21 (0.049)	0.059 (0.0115)	
PB	0.21 (0.027)	0.45 (0.061)		
S	0.99 (0.136)	0.36 (0.068)	1.23 (0.126)	0.72 (0.084)
PG			0.71 (0.063)	0.104 (0.0101)
PH-AR	1.29 (0.265)	2.64 (0.944)	3.26 (0.508)	
PH-AC	3.14 (1.036)	3.48 (1.498)	3.90 (0.835)	1.14 (0.148)
PT-AR	0.33 (0.066)	0.28 (0.046)	0.29 (0.094)	
PT-AC	0.17 (0.042)	0.37 (0.093)	0.28 (0.086)	
PB-AG	1.15 (0.370)	0.79 (0.118)		
S-AR	1.06 (0.201)	0.36 (0.047)	0.68 (0.088)	
S-AC	1.43 (0.607)	0.48 (0.074)	0.97 (0.157)	0.66 (0.082)
PG-AR			0.52 (0.045)	
PG-AC			0.76 (0.075)	0.20 (0.019)
AG	0.3 (2.37)	0.72 (0.146)		
AR	0.30 (0.029)	0.40 (0.044)	0.38 (0.023)	
AC	0.27 (0.061)	0.44 (0.092)	0.61 (0.092)	0.31 (0.024)

Table (xvii): Leaf magnesium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	3.42 (0.428)	2.78 (0.344)	6.29 (0.393)	1.58 (0.199)
PT	0.11 (0.015)	0.13 (0.018)	0.048 (0.0057)	
PB	0.32 (0.035)	0.62 (0.070)		
S	1.16 (0.155)	0.42 (0.079)	1.44 (0.144)	0.84 (0.097)
PG			0.73 (0.051)	0.142 (0.0106)
PH-AR	1.51 (0.350)	3.25 (1.352)	3.80 (0.631)	
PH-AC	3.39 (0.962)	3.68 (1.325)	4.29 (0.807)	1.27 (0.146)
PT-AR	0.29 (0.053)	0.22 (0.030)	0.25 (0.061)	
PT-AC	0.16 (0.032)	0.36 (0.078)	0.33 (0.089)	
PB-AG	1.71 (0.514)	1.07 (0.143)		
S-AR	1.24 (0.256)	0.40 (0.055)	0.79 (0.109)	
S-AC	1.58 (0.575)	0.60 (0.087)	1.13 (0.165)	0.78 (0.088)
PG-AR			0.55 (0.042)	
PG-AC			0.87 (0.076)	0.26 (0.020)
AG	9.7 (3.82)	1.09 (0.225)		
AR	0.32 (0.035)	0.45 (0.055)	0.41 (0.028)	
AC	0.35 (0.072)	0.56 (0.106)	0.76 (0.105)	0.40 (0.029)

Table (xviii): Above magnesium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	6.54 (0.810)	5.31 (0.651)	11.99 (0.743)	3.02 (0.378)
PT	0.30 (0.052)	0.35 (0.066)	0.110 (0.0176)	
PB	0.54 (0.061)	1.07 (0.126)	1.47(0.187)	
S	2.15 (0.281)	0.79 (0.144)	2.66 (0.261)	1.56 (0.175)
PG			1.42 (0.109)	0.248 (0.0205)
PH-AR	2.80 (0.590)	5.80 (2.123)	7.13 (1.132)	
PH-AC	6.60 (1.995)	7.23 (2.799)	8.30 (1.649)	2.44 (0.295)
PT-AR	0.64 (0.120)	0.52 (0.078)	0.56 (0.161)	
PT-AC	0.34 (0.076)	0.76 (0.175)	0.63 (0.182)	
PB-AG	2.89 (0.882)	1.85 (0.254)		
S-AR	2.28 (0.434)	0.78 (0.099)	1.47 (0.187)	
S-AC	2.98 (1.128)	1.09 (0.159)	2.09 (0.316)	1.45 (0.165)
PG-AR			1.07 (0.084)	
PG-AC			1.63 (0.149)	0.46 (0.039)
AG	16.2 (6.30)	1.84 (0.376)		
AR	0.63 (0.063)	0.85 (0.093)	0.80 (0.049)	
AC	0.63 (0.133)	1.01 (0.197)	1.38 (0.196)	0.71 (0.053)

Table (xix): Stem calcium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	620 (80)	490 (59)	1100 (68)	302 (37.1)
PT	84 (20.2)	97 (23.4)	25 (5.2)	
PB	77 (7.0)	138 (12.8)		
S	354 (41.7)	136 (20.7)	390 (34.9)	270 (26.7)
PG			52 (4.2)	7.8 (0.67)
PH-AR	300 (45)	550 (131)	670 (66)	
PH-AC	640 (138)	640 (169)	810 (112)	282 (28.3)
PT-AR	164 (36.9)	138 (24.6)	128 (43.3)	
PT-AC	82 (24.5)	189 (52.8)	136 (47.9)	
PB-AG	450 (136)	248 (29.5)		
S-AR	410 (68)	149 (17.9)	253 (28.3)	
S-AC	570 (232)	205 (30.7)	361 (56.0)	260 (28.4)
PG-AR			111 (14.3)	
PG-AC			199 (32.4)	82 (19.8)
AG	2400 (900)	270 (53)		
AR	147 (16.2)	207 (25.7)	179 (11.9)	
AC	129 (31.9)	208 (45.5)	320 (58)	154 (13.4)

Table (xx): Leaf calcium content in g × 10^{-3} per tree with standard error of mean in brackets. Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	670 (89)	530 (65)	1180 (75)	320 (40.8)
PT	49 (6.7)	54 (7.2)	20 (2.3)	
PB	62 (5.7)	111 (10.5)		
S	283 (31.8)	112 (16.3)	312 (26.7)	218 (20.4)
PG			92 (5.1)	22.4 (1.26)
PH-AR	300 (53)	580 (167)	700 (86)	
PH-AC	640 (136)	640 (161)	810 (114)	277 (26.3)
PT-AR	103 (17.7)	82 (10.1)	75 (14.5)	
PT-AC	59 (11.5)	128 (25.0)	102 (24.0)	
PB-AG	480 (164)	233 (29.0)		
S-AR	320 (54)	115 (13.7)	197 (22.1)	
S-AC	400 (124)	171 (22.8)	280 (36.1)	208 (19.3)
PG-AR			103 (6.8)	
PG-AC			191 (18.6)	69 (6.4)
AG	2500 (970)	290 (56)		
AR	109 (12.0)	153 (19.2)	132 (8.8)	
AC	113 (22.7)	173 (30.5)	250 (37)	135 (9.8)

Table (xxi): Total aboveground calcium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St Lambert	Villeroy	St Louis	Amos
PH	1310 (170)	1030 (125)	2300 (144)	529 (78.5)
PT	136 (26.0)	154 (29.0)	46 (7.4)	
PB	142 (12.3)	247 (21.9)		
S	640 (72.3)	253 (36.8)	704 (60.6)	491 (46.4)
PG			143 (8.8)	30.5 (1.93)
PH AR	600 (95)	1120 (280)	1380 (147)	
PH AC	1290 (273)	1290 (328)	1630 (226)	564 (54.6)
PT AR	272 (53.7)	226 (34.2)	207 (54.4)	
PT AC	143 (35.2)	321 (75.1)	240 (69.7)	
PB AG	920 (289)	474 (55.4)		
S AR	720 (118)	270 (31.4)	456 (49.3)	
S AC	950 (331)	380 (52.8)	640 (89.4)	469 (46.4)
PG AR			212 (17.7)	
PG AC			386 (45.7)	142 (17.9)
AG	4900 (1880)	570 (110)		
AR	264 (28.1)	367 (44.0)	320 (20.7)	
AC	244 (53.9)	384 (74.2)	570 (92)	291 (22.9)

Table (xxii): Stem calcium content in kg ha $^{-1}$ with standard error of mean in brackets. Fall 1982

	St Lambert	Villeroy	St Louis	Amos
PH	8 7 (1 11)	6 8 (0 82)	15 2 (0 94)	4 19 (0 516)
PT	1 16 (0 281)	1 35 (0 325)	0 35 (0 072)	
PB	1 07 (0 098)	1 91 (0 178)		
S	4 92 (0 579)	1 89 (0 288)	5 41 (0 484)	3 75 (0 371)
PG			0 72 (0 059)	0 108 (0 0093)
PH AR	4 2 (0 63)	7 6 (1 81)	9 3 (0 92)	
PH AC	8 8 (1 92)	8 9 (2 35)	11 2 (1 56)	3 92 (0 393)
PT AR	2 27 (0 513)	1 91 (0 341)	1 78 (0 602)	
PT AC	1 13 (0 340)	2 63 (0 733)	1 88 (0 666)	
PB AG	6 3 (1 88)	3 44 (0 410)		
S AR	5 7 (0 95)	2 07 (0 249)	3 52 (0 393)	
S AC	7 9 (3 22)	2 85 (0 427)	5 01 (0 777)	3 61 (0 395)
PG AR			1 54 (0 199)	
PG AC			2 77 (0 450)	1 14 (0 275)
AG	33 (12 5)	3 8 (0 734)		
AR	2 05 (0 224)	2 87 (0 357)	2 48 (0 165)	
AC	1 79 (0 444)	2 89 (0 631)	4 4 (0 80)	2 13 (0 186)

Table (xxiii): Leaf calcium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	9.3 (1.23)	7.3 (0.90)	16.4 (1.04)	4.45 (0.566)
PT	0.68 (0.093)	0.75 (0.100)	0.27 (0.031)	
PB	0.86 (0.079)	1.54 (0.146)		
S	3.94 (0.442)	1.56 (0.226)	4.33 (0.371)	3.02 (0.284)
PG			1.28 (0.071)	0.311 (0.0176)
PH-AR	4.2 (0.74)	8.0 (2.32)	9.8 (1.19)	
PH-AC	8.9 (1.89)	8.9 (2.23)	11.3 (1.59)	3.84 (0.366)
PT-AR	1.42 (0.246)	1.13 (0.141)	1.04 (0.201)	
PT-AC	0.82 (0.160)	1.77 (0.348)	1.41 (0.333)	
PB-AG	6.6 (2.28)	3.23 (0.402)		
S-AR	4.4 (0.75)	1.60 (0.190)	2.74 (0.307)	
S-AC	5.5 (1.72)	2.38 (0.316)	3.88 (0.502)	2.89 (0.268)
PG-AR			1.44 (0.094)	
PG-AC			2.65 (0.258)	0.96 (0.089)
AG	35 (13.4)	4.0 (0.78)		
AR	1.51 (0.167)	2.13 (0.266)	1.83 (0.122)	
AC	1.57 (0.316)	2.41 (0.424)	3.5 (0.52)	1.87 (0.136)

Table (xxiv): Total aboveground calcium content in kg ha $^{-1}$ with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	18.2 (2.36)	14.3 (1.74)	32.0 (1.99)	8.73 (1.091)
PT	1.89 (0.360)	2.14 (0.403)	0.64 (0.103)	
PB	1.98 (0.171)	3.44 (0.304)		
S	8.90 (1.004)	3.51 (0.512)	9.78 (0.842)	6.82 (0.644)
PG			1.98 (0.123)	0.423 (0.0269)
PH-AR	8.4 (1.32)	16 (3.9)	19.2 (2.04)	
PH-AC	17.9 (3.79)	17.9 (4.55)	22.7 (3.13)	7.83 (0.758)
PT-AR	3.78 (0.746)	3.14 (0.475)	2.87 (0.756)	
PT-AC	1.99 (0.489)	4.45 (1.042)	3.33 (0.968)	
PB-AG	12.8 (4.01)	6.58 (0.770)		
S-AR	10.1 (1.64)	3.75 (0.435)	6.33 (0.685)	
S-AC	13.2 (4.60)	5.28 (0.733)	8.89 (1.242)	6.51 (0.644)
PG-AR			2.95 (0.246)	
PG-AC			5.36 (0.635)	1.98 (0.249)
AG	68 (26.1)	7.9 (1.52)		
AR	3.67 (0.391)	5.10 (0.6111)	4.44 (0.287)	
AC	3.40 (0.748)	5.33 (1.030)	8.0 (1.28)	4.04 (0.318)

Table (xxv): Stem potassium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	660 (87)	530 (69)	1220 (80)	300 (40)
PT	39 (7.5)	47 (9.9)	13.9 (2.46)	
PB	47 (7.2)	111 (18.0)		
S	228 (33.1)	79 (16.0)	283 (30.6)	164 (20.5)
PG			162 (14.2)	24.2 (2.31)
PH-AR	270 (54)	570 (199)	710 (104)	
PH-AC	700 (263)	790 (392)	880 (213)	240 (34.4)
PT-AR	77 (14.9)	64 (10.0)	66 (19.8)	
PT-AC	34 (8.4)	74 (16.9)	51 (13.3)	
PB-AG	160 (41.0)	159 (26.1)		
S-AR	248 (48.2)	84 (11.4)	160 (21.1)	
S-AC	340 (168)	98 (15.6)	216 (39.4)	147 (20.4)
PG-AR			122 (10.5)	
PG-AC			163 (16.8)	40 (3.5)
AG	710 (215)	101 (17.4)		
AR	72 (7.2)	98 (10.8)	91 (5.6)	
AC	51 (11.9)	84 (18.2)	116 (18.1)	58 (4.7)

Table (xxvi): Leaf potassium content in g × 10^{-3} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	660 (128)	510 (98)	1320 (115)	260 (56)
PT	22 (3.4)	25 (4.3)	8.6 (1.22)	
PB	48 (11.2)	145 (38.2)		
S	189 (24.8)	69 (12.7)	234 (23.0)	138 (15.5)
PG			189 (15.1)	31.4 (2.72)
PH-AR	240 (56)	620 (292)	710 (119)	
PH-AC	660 (269)	740 (395)	890 (240)	193 (29.9)
PT-AR	62 (13.6)	46 (7.2)	56 (17.9)	
PT-AC	25 (5.5)	55 (12.4)	44 (11.8)	
PB-AG	149 (41.7)	206 (46.5)		
S-AR	215 (42.0)	75 (10.5)	141 (19.0)	
S-AC	290 (140)	88 (13.7)	186 (33.4)	125 (16.5)
PG-AR			133 (12.0)	
PG-AC			179 (19.7)	41 (3.3)
AG	530 (124)	93 (13.4)		
AR	67 (8.2)	97 (13.5)	86 (6.4)	
AC	46 (11.3)	77 (17.4)	107 (17.3)	52 (4.4)

Table (xxvii): Total aboveground potassium content in g × 10^{-3} per tree with standard error of mean in in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	1330 (205)	1050 (160)	2550 (188)	570 (92)
PT	63 (11.2)	75 (14.5)	23 (3.8)	
PB	97 (17.2)	248 (47.7)		
S	424 (58.6)	151 (29.2)	526 (54.2)	307 (36.4)
PG			350 (29.0)	56 (5.0)
PH-AR	520 (107)	1180 (450)	1430 (219)	
PH-AC	1400 (540)	1570 (801)	1800 (456)	444 (65.2)
PT-AR	145 (29.2)	115 (18.0)	128 (39.7)	
PT-AC	61 (14.2)	132 (29.7)	97 (25.2)	
PB-AG	304 (76.0)	351 (63.3)		
S-AR	470 (89.3)	164 (22.1)	308 (40.0)	
S-AC	640 (310)	189 (29.6)	409 (73.7)	277 (37.4)
PG-AR			257 (21.9)	
PG-AC			343 (36.0)	82 (6.8)
AG	1190 (306)	195 (29.8)		
AR	144 (15.5)	200 (23.8)	184 (12.1)	
AC	99 (23.3)	164 (35.7)	226 (35.5)	111 (9.1)

Table (xxviii): Stem potassium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	9.1 (1.21)	7.3 (0.96)	17.0 (1.11)	4.1 (0.56)
PT	0.54 (0.105)	0.65 (0.138)	0.19 (0.034)	
PB	0.66 (0.100)	1.54 (0.250)		
S	3.16 (0.460)	1.10 (0.223)	3.94 (0.425)	2.27 (0.285)
PG			2.25 (0.197)	0.34 (0.032)
PH-AR	3.8 (0.75)	8.0 (2.76)	9.8 (1.45)	
PH-AC	9.8 (3.66)	11.0 (5.44)	12.2 (2.96)	3.33 (0.477)
PT-AR	1.07 (0.207)	0.89 (0.139)	0.92 (0.275)	
PT-AC	0.48 (0.116)	1.02 (0.234)	0.72 (0.185)	
PB-AG	2.23 (0.570)	2.20 (0.362)		
S-AR	3.45 (0.670)	1.17 (0.159)	2.22 (0.293)	
S-AC	4.7 (2.34)	1.36 (0.217)	3.00 (0.548)	2.04 (0.284)
PG-AR			1.69 (0.146)	
PG-AC			2.27 (0.233)	0.55 (0.049)
AG	9.9 (2.99)	1.41 (0.241)		
AR	1.00 (0.010)	1.36 (0.151)	1.27 (0.078)	
AC	0.71 (0.166)	1.17 (0.253)	1.62 (0.252)	0.80 (0.065)

Table (xxix): Leaf potassium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	9.2 (1.78)	7.1 (1.36)	18.4 (1.60)	3.7 (0.78)
PT	0.30 (0.048)	0.35 (0.060)	0.12 (0.017)	
PB	0.66 (0.156)	2.01 (0.530)		
S	2.62 (0.345)	0.96 (0.176)	3.25 (0.320)	1.91 (0.215)
PG			2.62 (0.210)	0.44 (0.038)
PH-AR	3.3 (0.77)	8.6 (4.05)	9.9 (1.65)	
PH-AC	9.2 (3.74)	10.3 (5.49)	12.4 (3.34)	2.69 (0.416)
PT-AR	0.86 (0.189)	0.64 (0.101)	0.77 (0.248)	
PT-AC	0.34 (0.076)	0.76 (0.173)	0.60 (0.163)	
PB-AG	2.06 (0.580)	2.86 (0.646)		
S-AR	2.99 (0.583)	1.04 (0.145)	1.96 (0.264)	
S-AC	4.0 (1.94)	1.22 (0.191)	2.59 (0.463)	1.74 (0.229)
PG-AR			1.84 (0.166)	
PG-AC			2.49 (0.274)	0.57 (0.046)
AG	7.3 (1.72)	1.30 (0.186)		
AR	0.93 (0.114)	1.35 (0.187)	1.20 (0.089)	
AC	0.64 (0.156)	1.08 (0.242)	1.49 (0.241)	0.72 (0.061)

Table (xxx): Total aboveground potassium content in kg ha^{-1} with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	18.5 (2.85)	14.6 (2.23)	35.4 (2.61)	7.9 (1.28)
PT	0.88 (0.156)	1.04 (0.201)	0.32 (0.053)	
PB	1.35 (0.238)	3.44 (0.663)		
S	5.89 (0.814)	2.10 (0.405)	7.31 (0.753)	4.26 (0.505)
PG			4.87 (0.403)	0.78 (0.070)
PH-AR	7.3 (1.49)	16.4 (6.24)	19.8 (3.04)	
PH-AC	19.3 (7.50)	21.8 (11.12)	24.9 (6.33)	6.16 (0.905)
PT-AR	2.01 (0.405)	1.60 (0.251)	1.77 (0.552)	
PT-AC	0.84 (0.197)	1.83 (0.413)	1.34 (0.350)	
PB-AG	4.22 (1.056)	4.87 (0.880)		
S-AR	6.53 (1.241)	2.27 (0.307)	4.27 (0.556)	
S-AC	8.9 (4.31)	2.62 (0.411)	5.68 (1.023)	3.84 (0.519)
PG-AR			3.57 (0.305)	
PG-AC			4.77 (0.500)	1.13 (0.094)
AG	16.5 (4.25)	2.71 (0.414)		
AR	2.00 (0.215)	2.78 (0.331)	2.56 (0.168)	
AC	1.37 (0.324)	2.27 (0.496)	3.14 (0.493)	1.54 (0.126)

Table (xxxi): Total aboveground nitrogen content of hybrid poplars in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	189 (26.7) B	147 (19.4) B	338 (22.4) A	88 (12.1) D
PH-AR	135 (26.4) BC	270 (70.3) AB	288 (28.0) A	
PH-AC	257 (36.1) AB	237 (26.4) AB	330 (26.3) A	115 (14.3) CD

Table (xxxii): Total aboveground nitrogen content of *Populus tremuloides* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
PT	19 (3.8) AB	22 (4.3) AB	6 (1.1) C
PT-AR	26 (8.5) AB	33 (11.4) A	6 (1.2) C
PT-AC	16 (5.1) B	25 (7.0) AB	6 (1.3) C

Table (xxxiii): Total aboveground nitrogen content of *Populus balsamifera* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy
PB	28 (4.4) B	67 (11.3) A
PB-AG	22 (3.1) B	159 (54.2) A

Table (xxxiv): Total aboveground nitrogen content of *Salix alba* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
S	67 (7.8) AB	26 (3.9) B	74 (6.5) A	51 (5.0) AB
S-AR	119 (26.7) A	33 (6.9) B	68 (12.2) AB	
S-AC	96 (18.4) A	30 (5.6) B	73 (8.1) A	81 (11.9) AB

Table (xxxv): Total aboveground nitrogen content of *Pinus banksiana* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Louis	Amos
PG	117 (8.7) A	20 (1.5) B
PG-AR	111 (13.7) A	
PG-AC	110 (7.9) A	19 (1.4) B

Table (xxxvi): Total aboveground nitrogen content of *Alnus glutinosa* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy
AG	940 (262) A	144 (22.4) C
AG-PB	520 (206) A	146 (21.0) BC

Table (xxxvii): Total aboveground nitrogen content of *Alnus rugosa* in g × 10^{-2} per tree with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
AR	81 (7.8) B	109 (11.7) B	98 (5.7) B
AR-PH	78 (11.2) B	97 (19.4) B	133 (11.4) A
AR-PT	99 (18.9) B	66 (7.2) B	93 (10.1) B
AR-S	102 (15.4) B	74 (9.0) B	92 (9.8) B
AR-PG			92 (7.0) B

Table (xxxviii): Total aboveground nitrogen content of *Alnus crispa* with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis
AC	63 (13.9) CD	98 (19.1) BC	147 (23.7) AB
AC-PH	92 (19.9) BC	77 (18.4) CD	143 (21.1) AB
AC-PT	47 (18.5) D	126 (41.6) ABC	104 (28.8) BC
AC-S	117 (B1.4) ABC	116 (23.9) ABC	123 (30.5) ABC
AC-PG			210 (44.9) A

Table (xxxix): Weight in g per leaf of the upper leaves[1] with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	0.58 (0.038)	0.72 (0.113)	0.47 (0.029)	0.17 (0.016)
PT	0.12 (0.012)	0.12 (0.014)	0.05 (0.003)	
PB	0.29 (0.027)	0.40 (0.037)		
S*	0.45 (0.027)	0.33 (0.014)	0.22 (0.009)	0.31 (0.015)
PG*			1.00 (0.026)	0.82 (0.061)
AG	0.49 (0.038)	0.27 (0.022)		
AR	0.28 (0.009)	0.22 (0.015)	0.33 (0.09)	
AC	0.19 (0.011)	0.16 (0.011)	0.22 (0.007)	0.17 (0.006)

* *Salix alba*, average weight of 10 leaves; *Pinus banksiana*, average weight of 100 leaves.

[1] 3rd and 4th leaves for all species except *Salix* (3th, 4th, 5th leaves), and *Pinus banksiana* (current growth)

Table (xxxx): Nitrogen content of the upper leaves in % with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	1.36 (0.054)	1.52 (0.150)	1.27 (0.031)	1.78 (0.046)
PT	2.09 (0.063)	2.24 (0.069)	2.02 (0.063)	
PB	1.84 (0.102)	2.13 (0.102)		
S	1.97 (0.092)	1.96 (0.092)	2.01 (0.072)	2.39 (0.094)
PG			1.81 (0.017)	1.79 (0.039)
AG	3.16 (0.112)	3.31 (0.16)		
AR	2.75 (0.071)	2.82 (0.053)	3.13 (0.037)	
AC	2.60 (0.078)	2.77 (0.103)	3.30 (0.029)	2.88 (0.039)

Table (xxxxi): Phosphorus content of the upper leaves in PPM with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	1100 (33)	1820 (91)	2080 (70)	2080 (95)
PT	1520 (61)	2210 (66)	2780 (85)	
PB	1280 (74)	2470 (145)		
S	1650 (52)	2380 (146)	2830 (109)	2640 (96)
PG			1470 (16)	1570 (35)
AG	1570 (73)	2060 (84)		
AR	1620 (54)	1660 (71)	1780 (35)	
AC	1320 (35)	1610 (51)	1860 (36)	1470 (27)

Table (xxxxii): Magnesium content of the upper leaves in ppm with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	4460 (183)	2060 (145)	2590 (93)	3180 (167)
PT	2700 (231)	1930 (117)	2180 (130)	
PB	3550 (253)	2630 (190)		
S	5490 (530)	2650 (184)	3090 (123)	3510 (133)
PG			1210 (16)	1400 (45)
AG	2610 (162)	1760 (184)		
AR	1870 (97)	970 (73)	1860 (37)	
AC	2130 (127)	1170 (80)	2120 (55)	2220 (94)

Table (xxxxiii): Calcium content of the upper leaves in ppm with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	6880 (177)	2300 (128)	2990 (108)	5810 (616)
PT	12840 (520)	9690 (502)	12850 (418)	
PB	10030 (666)	4290 (306)		
S	10910 (416)	7990 (549)	5240 (363)	8420 (1063)
PG			1410 (34)	2050 (138)
AG	5850 (631)	6020 (402)		
AR	5330 (171)	3490 (194)	5380 (209)	
AC	6980 (378)	4700 (173)	7380 (247)	7080 (163)

Table (xxxxiv): Potassium content of the upper leaves in ppm with standard error of mean in brackets, Fall 1982

	St-Lambert	Villeroy	St-Louis	Amos
PH	3920 (242)	7620 (507)	12290 (407)	9370 (426)
PT	4650 (261)	5460 (197)	6970 (320)	
PB	5280 (409)	6970 (612)		
S	5570 (480)	6600 (552)	21330 (862)	15050 (982)
PG			3990 (74)	4200 (148)
AG	4440 (264)	4040 (376)		
AR	4380 (265)	3760 (306)	5850 (147)	
AC	4210 (216)	4210 (311)	6540 (157)	4320 (103)

APPENDIX IV

Codes:

A: Black alder

P: Hybrid poplar (in the field) and aspen (in the glasshouse)

AP: Poplar and alder proportionally to the ratio

Δ leaf + stem: Variation between stems + leaves of autumn and stems of spring.

Lower case letters (a to e) indicate significant differences when different letters follow data (Dunn's Test).

Table (i): Production of biomass in the field experiment on the campus of Laval University for spring 1982 (individual plant)

Spacing (cm)	Species ratio	Dry weight of stems (g)		
		P	A	AP
33	3A	–	21c	21b
	2A 1P	26a,b[1]	19c	21b
	1A 2P	27b,c	18c	24c
	3P	9c	–	9c
66	3A	–	25b	25a
	2A 1P	35a	19c	23b
	1A 2P	23c	33a	27b
	3P	22b,c	–	22c
99	3A	–	21b,c	21a,b
	2A 1P	11c	22b,c	19b
	1P 2P	21a,b	21b,c	21b
	3P	25a,b	–	25b,c

A = *Alnus glutinosa*
P = Hybrid poplar
[1] = Dunn's Test (0.3 for AP; 0.225 for A & P)

Table (ii): Production of biomass in the field experiment on the campus of Laval University for autumn 1982 (individual plant)

Spacing (cm)	Species ratio	Biomass – dry weight (g)								
		leaf			stem			leaf + stem		
		P	A	AP	P	A	AP	P	A	AP
33	3A	–	23d	23d	–	83d	83cd	–	106c	106c,d
	2A 1P	40a	25d	29d	152a	87d	104b,c	192a	112c	133b,c,d
	1A 2P	27b	24d	26d	108b	78d	95c,d	135b	102c	121c,d
	3P	14c	–	14d	52c	–	52e	66c	–	66e
66	3A	–	64b,c	64a	–	122c	122a,b	–	186b	186a
	2A 1P	45a,b	52c	51b,c	106b	100c,d	101c,d	151b	153b,c	152b,c
	1A 2P	44a,b	106a	79a,b	105b	207a	163a,b	150b	313a	242a
	3P	34b	–	34d	82b	–	82d,e	116b	–	116d
99	3A	–	80a,b	80a	–	156a,b	156a	–	237a	237a
	2A 1P	25b,c	73a,b,c	66b	63b,c	142b,c	130a,b	88b,c	215a,b	196a,b
	1A 2P	21b,c	56b,c	41c,d	53b,c	108c,d	84c,d,e	74b,c	165b,c	125c,d
	3P	54a,b	–	54b,c,d	126a,b	–	126b,c,d	180a,b	–	180b,c,d

Table (iii): Production of biomass in the field experiment on the campus of Laval University during summer 1982 (individual plant)

Spacing (cm)	Species ratio	Biomass – dry weight (g)					
			Δ stem			Δ leaf + stem	
		P	A	AP	D	A	AP
33	3A	–	62c	62d,e	–	85c	85d,e
	2A 1P	126a	68c	83d	166a	93c	112c,d
	1A 2P	81b,c	60c	71d,e	108b,c	84c	97d,e
	3P	43d	–	43e	57d	–	57f
66	3A	–	97a,b	97a,b	–	161d	161b
	2A 1P	71a,b,c	81b,c	78b,c	116b,c	134b	129b,c,d
	1A 2P	82a,b,c	174a	136a,b	127b,c	280a	215a,b
	3P	60a,b,c	–	60c	94b,c,d	–	94e,f
99	3A	–	135a	135a	–	216a	216a
	2A 1P	52b,c,d	120a,b	111a,b,c	77b,c,d	193a,b	177b,c
	1A 2P	32c,d	87b,c	63c	53c,d	144b	104d,e,f
	3P	101a,b	–	101a,b,c	155a,b	–	155b,c

Table (iv): Production of biomass in the field experiment on the campus of Laval University for spring 1982 (per hectare).

Spacing (cm)	Species ratio	Dry weight of stems (kg ha^{-1})		
		P	A	AP
33	3A	–	1900a	1900a
	2A 1P	560a,b	1100b	1660a
	1A 2P	1200a	530c	1730a
	3P	740a,b	–	740b
66	3A	–	490c	490b
	2A 1P	170b	230d	400b
	1A 2P	170b	220d	390b
	3P	280b	–	280b
99	3A	–	200d	200b
	2A 1P	22b	150d	172b
	1A 2P	85b	67d	152b
	3P	140b	–	140b

Table (v): Production of biomass in the field experiment on the campus of Laval University for autumn 1982 (per hectare).

Spacing (cm)	Species ratio	Biomass – dry weight (kg ha^{-1})								
		leaf			stem			leaf + stem		
		P	A	AP	P	A	AP	P	A	AP
33	3A	–	2100a	2100a	–	7600a	7600a	–	9700a	9700a
	2A 1P	820a,b	1400b	2220a	3100a,b	4800b	7900a	3920a,b	6200b	10120a
	1A 2P	1100a	690d	1790a,b	4300a	2300c	6600a	5400a	2990c,d	8390a
	3P	1000a	–	1000b,c,d	3800a	–	3800b	4800a	–	4800b
66	3A	–	1200b,c	1200b,c	–	2300c	2300b,c	–	3500c	3500b,c
	2A 1P	150b,c	620d,e	770c,d	360c	1200c,d	1560b,c	510b,c	1820c,d,e	2330b,c
	1A 2P	210b,c	680d	890c,d	500c	1300c,d	1800b,c	710b,c	1980c,d,e	2690b,c
	3P	310b,c	–	310d	750b,c	–	750c	1060b,c	–	1060c
99	3A	–	740c,d	740c,d	–	1400c,d	1400b,c	–	2140c,e	2140b,c
	2A 1P	32c	470d,e	502c,d	78c	910d	988c	110c	1380d,e	1490b,c
	1A 2P	46c	170e	216d	120c	330d	450c	166c	500e	666c
	3P	200b,c	–	200d	470c	–	470c	670b,c	–	670c

Table (vi): Biomass increment in the field experiment on the campus of Laval University during summer 1982 (per hectare).

Spacing (cm)	Species ratio	Δ stem			Δ leaf + stem		
		P	A	AP	P	A	AP
33	3A	–	5700a	5700a		7800a	7800a
	2A 1P	2540a	3700b	6240a	3360a	5100b	8460a
	1A 2P	3100a	1770c,d	4870a	4200a	2460c,d	6660a
	3P	3060a	–	3060a	4060a	–	4060b
66	3A	–	1810c	1810b,c	–	3010c	3010b,c
	2A 1P	190b	970c,d,e	1160b,c	340b	1590c,d,e	1930b,c
	1A 2P	330b	1080c,d,e	1410b,c	540b	1760c,d,e	2300b,c
	3P	470b	–	470c	780b	–	780c
99	3A	–	1200c,d	1200b,c	–	1940c,d	1940b,c
	2A 1P	56b	760d,e	816c	88b	1230d,e	1318b,c
	1A 2P	35b	263e	298c	81b	433e	514c
	3P	330b	–	330c	530b	–	530c

Table (vii): Uptake of nitrogen in the field experiment on the campus of Laval University for spring 1982 (individual plant)

Spacing (cm)	Species ratio	Nitrogen mineralomass of stems (g)		
		P	A	AP
33	3A		0.34c	0.34a,b
	2A 1P	0.18a,b	0.31c	0.28c,d
	1A 2P	0.19b,c	0.28c	0.22e,f
	3P	0.06c	–	0.06h
66	3A	–	0.40b	0.40a
	2A 1P	0.24a	0.31c	0.29b,c
	1A 2P	0.15c	0.53a	0.32c,d
	3P	0.15b,c	–	0.15g,h
99	3A	–	0.33b,c	0.33a,b
	2A 1P	0.07c	0.35b,c	0.29b,c
	1A 2P	0.14a,b	0.33c	0.22d,e
	3P	0.17a,b	–	0.17f,g

Table (viii): Uptake of nitrogen in the field experiment on the campus of Laval Univeristy for autumn 1982 (individual plant).

		Mineralomass of nitrogen (g)								
Spacing (cm)	Species ratio	Leaf			Stem			Leaf + Stem		
		P	A	AP	P	A	AP	P	A	AP
33	3A	–	0.72d	0.72d	–	0.61c	0.61c,d	–	1.33d	1.33d
	2A 1p	0.65a	0.76d	0.73d	0.51a	0.64c	0.61c,d	1.16a	1.40d	1.34d
	1A 2P	0.44a	0.74d	0.56d	0.40a,b	0.59c	0.48e	0.84b	1.33d	1.04d
	3P	0.23b	–	0.23e	0.20c	–	0.20f	0.43c	–	0.43e
66	3A	–	2.04b,c	2.04a	–	0.85b	0.85a,b	–	2.89b,c	2.89a
	2A 1P	2.27a	1.67c	1.80b,c	0,49a,b	0.73b,c	0.68c,d	2.76b	2.40c	2.48b,c
	1A 2P	1.97a	3.70a	2.95a,b	0.49a,b	0.81a	0.67b,c	2.46b	4.51a	3.62a,b
	3P	1.31a	–	1.31d	0.38a,b	–	0.38e	1.69b	–	1.69d
99	3A	–	2.63a,b	2.63a	–	0.99a	0.99a	–	3.62a,b	3.62a
	2A 1P	0.78a,b	2.40a,b,c	2.15a,b	0.29a,b,c	0.87a,b	0.78b,c	1.07b,c	3.27a,b,c	2.93a,b
	1A 2P	0.58a,b	1.81b,c	1.28c,d	0.24b,c	0.74b,c	0.52d,e	0.82b,c	2.55b,c	1.80d
	3P	2.77a	–	2.77c,d	0.58a,b	–	0.58d,e	3.35a,b	–	3.35c,d

Table (ix): Uptake of nitrogen in the field experiment on the campus of Laval University during summer 1982 (individual plant)

Spacing (cm)	Species ratio	Mineralomass of nitrogen (g)					
		Δ stem			Δ leaf + stem		
		P	A	AP	P	A	AP
33	3A	–	0.27d	0.27d,e	–	0.99c	0.99d
	2A 1P	0.33a	0.33c,d	0.33c,d	0.98a	1.09c	1.06d
	1A 2P	0.21a,b	0.31c,d	0.26d,e	0.65b,c	1.05c	0.82d
	3P	0.14c	–	0.14f	0.37d	–	0.37e
66	3A	–	0.45b	0.45b	–	2.49b	2.49a,b
	2A 1P	0.25b,c	0.42b,c	0.39b,c,d	2.52a,bc	2.09b	2.19c
	1A 2P	0.34b,c	0.28d	0.35b,c	2.31a,b,c	3.98a	3.30b,c
	3P	0.23b,c	–	0.23e,f	1.54a,b,c	–	1.54d
99	3A	–	0.66a	0.66a	–	3.29a	3.29a
	2A 1P	0.22a,b,c	0.52a,b	0.49b	1.00b,c,d	2.92a,b	2.64a,b,c
	1A 2P	0.10c	0.41b,c	0.30d,e	0.68c,d	2.22b	1.58d
	3P	0.41a,b	–	0.41c,d,e	3.18a,b	–	3.18c,d

Table (x): Uptake of nitrogen in the field experiment on the campus of Laval University for spring 1982 (per hectare)

Spacing (cm)	Species ratio	Nitrogen mineralomass of stems (kg ha^{-1})		
		P	A	AP
33	3A	–	30a	30a
	2A 1P	4a,b	18b	22a
	1A 2P	9a	8c	17a
	3P	5a,b	–	5b
66	3A	–	8c	8b
	2A 1P	1b	4d	5b
	1A 2P	1b	3d	4b
	3P	2b	–	2b
99	3A	–	3d	3b
	2A 1P	0b	2d	2b
	1A 2P	1b	1d	2b
	3P	1b	–	1b

Table (xi): Uptake of nitrogen-mineralomass in the field experiment on the campus of Laval University for autumn 1982 (per hectare)

Spacing (cm)	Species ratio	Mineralomass of nitrogen (kg ha^{-1})								
		Leaf			Stem			Leaf + Stem		
		P	A	AP	P	A	AP	P	A	Ap
33	3A	–	65a	65a	–	55a	55a	–	120a	120a
	2A 1P	13a,b	43b	56a,b	10a,b	36b	46a	23a,b,c	79b	102a
	1A 2P	18a	21c,d,e	39b,c	16a	17c	33b	34a	38c,d	72b
	3P	16a,b	–	16d,e	14a	–	14c	30a,b	–	30c,d
66	3A	–	38b,c	38b,c	–	16c	16c	–	54c	54b,c
	2A 1P	8a,b	20d,e	28c,d,e	2c	9d	11c,d	10b,c	29d,e	39c,d
	1A 2P	10a,b	23c,d	33c,d	2c	5d	7c,d	12a,b,c	28d,e	40c,d
	3P	12a,b	–	12d,e	4b,c	–	4d	16a,b,c	–	16d
99	3A	–	24c,d	24c,d,e	–	9d	9c,d	–	33c,d	33c,d
	2A 1P	1b	16d,e	17d,e	0c	6d	6c,d	1c	22d,e	23d
	1A 2P	1b	5e	6e	1c	2d	3d	2c	7e	9d
	3P	10a,b	–	10e	2c	–	2d	12a,b,c	–	12d

Table (xii): Production of nitrogen-mineralomass in the field experiment on the campus of Laval University during summer 1982 (per hectare)

Spacing (cm)	Species ratio	Mineralomass of nitrogen (kg ha^{-1}) Δ stem P	Δ stem A	Δ stem AP	Δ leaf + stem P	Δ leaf + stem A	Δ leaf + stem AP
33	3A	–	25a	25a	–	90a	90a
	2A 1P	6a	18b	24a	19a,b	61b	80a
	1A 2P	7a	9c	16b	25a	30c,d	55b
	3P	9a	–	9c	25a	–	25c,d,e
66	3A	–	8c	8c,d	–	46b,c	46b,c
	2A 1P	1b	5c,d,e	6c,d,e	9a,b	25d,e	34b,c,d,e
	1A 2P	1b	2d,e	3d,e	11a,b	25d,e	36b,c,d
	3P	2b	–	2e	14a,b	–	14d,e
99	3A	–	6c,d	6c,d,e	–	30c,d	30b,c,d,e
	2A 1P	0b	4d,e	4d,e	1b	20d,e	21d,e
	1A 2P	0b	1e	1e	1b	6e	7e
	3P	1b	–	1e	11a,b	–	11d,e

TABLE (xiii): Concentration of NO_3^--N in lysineters in the field expriments at Laval University.

Species ratio	NO_3^- (ppm)
3A	15a
2A 1P	7b
1A 2P	4b
3P	0.5b

P.S. Ammonium (NH_4^+) concentration was very low compared to nitrate (NO_3^-) and presented no particular trend.

Table (xiv): ^{15}N-analyses of different systems evaluating nitrogen fixation by alder in field experiments at Laval University

Treatment	^{15}N % A	δ
Soil	0.36928	8.0
N-Non-Fixing alder in Soil	0.36607	– 0.7
N-Fixing alder in Soil	0.36504	– 3.5
N-Fixing alder only	0.36454	– 4.9